Schizotypy and facial emotion processing

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I hereby declare that this thesis has not been and will not be, submitted in whole or in part to another University for the award of any other degree.

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PhD Psychology

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BRIEF SYNOPSIS

The ability to accurately interpret facial emotion is crucial to social being and our capacity to correctly interpret threat-related expressions has obvious adaptive value. Healthy individuals appear to process facial emotions rapidly, accurately and effortlessly, while individuals with schizophrenia often present with marked impairment in emotion processing. The hypothesis of continuity between schizophrenia and normal behaviour suggests that the signs and symptoms of the disorder also occur to varying, lesser degrees in the general population. This thesis presents a series of studies that explore the limits of facial emotion processing in healthy individuals, and its relationship with schizotypal personality traits.

The first paper describes a set of three studies that use eye tracking techniques to explore the limits of rapid emotion processing. It is shown that we can quickly orient attention towards emotional faces even when the faces are task-irrelevant, presented for very brief intervals, and located well into peripheral vision. The remaining studies explore whether high schizotypes have similarities to individuals with schizophrenia in the way that they process facial emotion. High schizotypes were significantly less accurate at discriminating facial emotions and significantly more likely to misperceive neutral faces as angry, offering support for continuum models of visual hallucinatory experiences. A further study revealed that high relative to low schizoptypes feel as though they are exposed to angry faces for longer. It is argued that this experience itself may serve to maintain hypervigilance to social threat. Finally, laterality biases during face perception were explored. Contrary to the predictions of continuum models of schizophrenia, high schizotypes had an increased left side / right hemisphere bias for face processing.

In summary, the thesis offers partial support for the hypothesis of continuity between the impairments in emotion discrimination observed in individuals with schizophrenia, and normal, healthy variation in facial emotion processing.

INCORPORATION OF PUBLISHED WORK

All of the papers presented in this thesis have been accepted for publication in peer-reviewed journals and the versions presented here are the final published or in press manuscripts. The papers reflect my own work (with supervisory input from the second author). I wrote the first draft and I took the lead on all subsequent revisions including those suggested as part of the peer-review process. Full references are detailed below:

Coy, A. L., & Hutton, S. B. (2012). The influence of extrafoveal emotional faces on prosaccade latencies. *Visual Cognition*, *20*(8), 883-901.

Coy, A. L., & Hutton, S. B. (2012). Misperceiving facial affect: effects of laterality and individual differences in susceptibility to visual hallucinations. *Psychiatry Research*, *196*(2-3), 225-229.

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CONTENTS

THESIS OVERVIEW

General Introduction

The ability to accurately read faces is critical to our existence as social beings. We rely heavily upon information from faces during social interaction both to identify people and to correctly interpret their emotions and intentions. Furthermore, the capacity to attend swiftly to threat-related (e.g., angry or fearful) faces has obvious adaptive value in that it allows for a more rapid defensive response to impending threat or danger in the environment. It is therefore unsurprising that the human brain is highly specialised for face and emotion processing. Converging research, for example, shows that when emotional and non-emotional stimuli are presented, emotionally charged stimuli such as expressive faces are encoded preferentially (Alpers & Gerdes, 2007) and are processed by dedicated distributed neural systems (see Adolphs, 2002; Adolphs, Damasio, Tranel & Damasio, 1996; Murphy *et al*., 2003). The human brain is so highly specialised for emotion processing that we are able to identify the emotion depicted by faces extremely rapidly (e.g., Smith, 2012) and usually with very little apparent effort, despite the constraints of our limited visual processing resources, particularly in terms of spatial acuity and attention (see Bayle, Henaff & Krolak-Salmon, 2009).

The visual environment is often extremely complex with many elements of a scene competing for limited visual attention, yet there is evidence that faces can recruit visual attention in less than 150 ms even when presented alongside other competing stimuli. Crouzet, Kirchner, and Thorpe (2010), for example, presented images of faces and vehicles either side of a central fixation cross and asked participants to make an eye movement (saccade) as quickly as possible to the image belonging to a pre-specified target category (face or vehicle). Saccades to faces were initiated on average in 138 ms, significantly faster than the average saccade latency to vehicles (167 ms). The fastest saccades to faces were initiated in as little as 110 ms. Since the stimuli were presented either to the left or right visual field (with 1.6° between the fixation cross and the inner edge of the stimuli), those visual properties of the face stimuli that fed into saccade programming to exert the observed speeding effect were processed, by their very nature, in non-foveal areas of the retina. This is particularly interesting because the concentration of receptors in the retina is not uniform, and visual acuity is therefore not constant across our entire visual field (see Wade & Swanston, 2001). By far the greatest concentration of cones is contained in the comparatively small foveal region of the retina, and there are far fewer cones in the surrounding parafoveal region with virtually none at all in the peripheral retina (Wade & Swanston, 2001). There is, as a consequence, greatest visual acuity for the comparatively small fixated region of the visual field that falls on the fovea and acuity diminishes sharply with increasing eccentricity from the fovea. Despite this diminished acuity, Crouzet, Kirchner, and Thorpe (2010) demonstrate that some information from faces can be encoded in just over 100 ms and that this information can be used to guide and speed up subsequent prosaccades.

In order to focus our limited processing resources on those regions of the visual scene that contain the most salient or useful information (given our current behavioural goals), we make two to three saccades per second. A saccadic eye movement to a specific spatial location is preceded by a covert (without moving the eyes) shift of attention to this region in space (Posner, 1980; Hoffman, 1998). Saccades are interspersed with fixations, during which the image on the retina is sufficiently still to be processed. Eye movements are therefore intimately linked with the concept of attention – and the location and duration of fixations made whilst people view a given scene are generally assumed to reflect (in a reasonably transparent way) which aspects of the scene the participants have attended. It is generally agreed that a combination of both exogenous factors (such as a sudden change in luminance) and endogenous factors (such as expectations or memories of an object's location) combine to influence the location of each fixation (see Hutton, 2008 for a review).

The full extent and the limits of our ability to encode information from faces presented in non-foveal locations are not yet fully understood. For example, how do specific properties of the nonfoveally presented face stimuli such as contrast or luminance affect prosaccades and how do task instructions influence the speed and accuracy of saccades to distal faces? What types of visual information can be extracted from parafoveal locations (e.g., overall gist of the stimulus versus fine details) and then used to guide saccades, and just how far into peripheral vision can faces influence saccade latencies and landing points? Do these limits vary systematically by the emotional expression on the faces? Given the adaptive value of identifying threat-related emotions, are these limits greater for angry or fearful faces than for facial emotions that do not communicate threat-related information? A fuller understanding of some of these issues is extremely important if we are to grasp the fundamental role of attention allocation in interacting adaptively with the environment. Where we attend to in a given scene reflects, reasonably transparently, which information we have chosen to process and individual differences in how attention is allocated may reflect variation in how scenes are interpreted- this inevitably has very important social implications.

Despite the evolution of rapid and specialised processing of faces and facial emotions in humans, there are of course circumstances when the face processing system fails to perform efficiently and the consequences can be profound. The failure to accurately recognise and interpret the emotions of others is one of the most enduring and pervasive deficits associated with schizophrenia (Morris, Weikert, & Loughland, 2009) and is directly related to symptom severity (Hofer *et al*., 2009) and outcome measures such as occupational functioning and independent living (Kee, Green, Mintz, & Brekke, 2003).

Schizophrenia is a clinical diagnosis of a psychosis characterised by syndromes of psychotic symptoms. According to the *Diagnostic and Statistical Manual of Mental Disorders, 4th Ed., text rev* (*DSM-IV-TR*) definition of schizophrenia, two or more of the following symptoms must be present for a significant portion of a one month period to reach a diagnosis of schizophrenia: delusions (e.g., persecutory, grandeur), hallucinations (e.g., auditory, visual, olfactory), odd / disorganised behaviour, disorganised speech, catatonic behaviour (e.g., unusual motor movements), one or more negative symptoms (e.g., low or flattened mood, alogia, apathy / low drive) (DSM–IV–TR; American

Psychiatric Association, 2000). Schizophrenia is also associated with stable cognitive impairment which is unrelated to positive symptoms (delusions, hallucinations, odd / disorganised behaviour, disorganised speech, catatonic / disorganised behaviour) of the disorder (see Harrison, Geddes & Sharpe, 2005). Individuals with schizophrenia, for example, often present with marked impairment in discriminating facial expressions of emotion, but the precise nature of their impairment is not yet fully understood (Mandal, Pandey, & Prasad, 1998 for a review). One possible explanation is that individuals with schizophrenia, in contrast to healthy controls, do not allocate attention optimally to faces. A number of studies using eye tracking techniques, for example, have revealed that, in contrast to controls, schizophrenia patients attended less to the most salient and informative features of faces, such as the eyes and mouth (Williams, Loughland, Gordon, & Davidson, 1999). Improving our understanding of the mechanisms underlying impaired emotion detection in schizophrenia is fundamental to designing and informing effective treatment and remediation therapies for the amelioration of social difficulties in schizophrenia.

In addition to impairments in accurately detecting and optimally attending to facial emotions, there is also some evidence to suggest that individuals with schizophrenia show particular error patterns when attempting to identify facial emotion- specifically, patients as compared to healthy controls are more likely to make false positive errors (seeing emotions in neutral faces) (e.g., Brown & Cohen, 2010). The precise pattern of false positive errors common in those with psychosis has not, however, been fully elucidated. Whether or not individuals with schizophrenia are more likely to misattribute threat-related emotions to faces, and how this possibly relates to particular positive symptoms such as hallucinations and paranoia, as well as comorbid anxiety and a state of long-term hypervigilance, has not been fully explored. Repeatedly interpreting neutral faces as angry, for example, will likely leave an individual feeling under threat, disliked or confused. Given the pervasiveness of persecutory delusions and false beliefs about the intentions of others (e.g., that other people pose an imminent threat) associated with psychosis, research in this area is extremely important. If further research identifies very specific error types when processing facial emotions associated with particular symptoms of schizophrenia, then interventions and treatments can be created that are aimed specifically at reducing these types of errors during social interaction, thus increasing the likelihood of improving functional outcome.

Many researchers agree that liability for schizophrenia can be expressed in ways other than full-blown schizophrenia. The “hypothesis of continuity” between schizophrenia and normal behaviour suggests that the signs and symptoms of the disorder, such as difficulties processing facial emotion, also occur to varying, lesser degrees in the general population (Claridge, 1997). The term “schizotypy”, which was first coined by Rado in 1953, describes this variation in schizophrenia liability across the general population. Those who exhibit more psychosis-like behaviours are referred to as high “schizotypes” or as being high in schizotypy. There is a large body of evidence in support of this symptomatic continuum between normal functioning and those behaviours such as benign referential thinking, hallucinatory-like experiences or non-symptomatic odd / eccentric behaviour associated with psychosis (see Claridge, 1997; Eckblad & Chapman, 1983; Johns & Van Os, 2001; Verdoux and van Os, 2002). Healthy individuals who experience hallucination-like experiences, for example, are at higher risk for developing a schizophrenia spectrum disorder than individuals who do not have such experiences (see Kelleher & Cannon, 2011 for a review). In addition, a large literature has shown that the information processing deficits associated with schizophrenia are also present, albeit less severely, in high schizotypes (e.g. Barrantes-Vidal *et al*, 2003; Park, Holzman & Lenzenweger, 1995). Johns and Van Os (2001) postulate that there may be a threshold at which those benign, non-symptomatic psychotic traits associated with high schizotypy become pathological and require treatment (but see work by Mohr and colleagues). In line with stress-diathesis models of psychiatric illness (see Walker & Diforio, 1997), the threshold may be lowered by increased stress levels (Williams, Henry & Green, 2007).

It is argued that the onset of schizophrenia precedes the commencement of symptomatic psychotic behaviours and that high schizotypes represent “a valid, albeit nonpsychotic, expression of the same liability that underpins schizophrenia" (Lenzenweger, 2010, p.17). It has further been argued that it is important to consider in psychosis research, groups other than individuals with diagnoses of schizophrenia (who form the very extremity of the psychosis continuum) (see Johns & Van Os, 2001; Lenzenweger, 2010). Considering, for example, healthy individual variation in psychotic-like behaviour (schizotypy), individuals at-risk for psychosis, and those who exhibit symptomatic behaviour associated with full-blown psychosis (under the acknowledgement that the boundaries of each of these "stages" are not clearly demarcated) will enhance understanding of the dynamics of the vulnerability continuum for schizophrenia spectrum disorders.

There are numerous questionnaires devised to assess individual differences in schizotypy. Descriptions of the most frequently used measures of schizotypy are detailed below in Table 1. The development of these inventories has confirmed that schizotypy is a multidimensional construct and that there are parallels between the multiple dimensions of schizotypy and the positive, negative and disorganised symptom clusters of schizophrenia (Claridge, 1997). The measures are clearly wide-ranging and this variety enables researchers to tap into selective components of schizoptypy. An inevitable consequence of these numerous scales, however, is that it makes valid comparison across studies using different measures of schizotypy difficult.

Questionnaire	Description	Response	Reference
Physical Anhedonia Scale	A 61-item inventory measuring deficit in the ability to experience pleasure from typically pleasurable physical stimuli.	True/False	Chapman, Chapman, and Raulin, 1976
Social Anhedonia Scale	A 48-item scale devised to measure deficit in the ability to experience pleasure from social interaction or exposure to social stimuli.	True/False	Chapman, Chapman and Raulin, 1976
Perceptual Aberration Scale	A 35-item scale which assesses psychotic-like perceptual aberration such as somatic distortions and hallucinations.	True/False	Chapman, Chapman, and Raulin, 1978
Launay Slade Hallucination Scale	A 12-item measure of predisposition towards hallucination and delusional ideation.	True/False	Launay and Slade, 1981
Revised Social Anhedonia Scale	A shortened 40 item version of the original 1976 scale with the original items tapping social anxiety removed.	True/False	Eckblad, Chapman, Chapman, Mishlove, 1982
Magical Ideation Scale	A 30-item measure of propensity to nonscientific belief, often related to causation.	True/False	Eckblad and Chapman, 1983

Impulsive Nonconformity Scale	A 51-item questionnaire designed to measure impulsive antisocial behaviour.	True/False	Chapman, Chapman, Numbers *et al*., 1984
The Intense Ambivalence Scale	A 45-item measure of the tendency to simultaneously experience conflicting feelings or desires.	True/False	Raulin, 1984
Launay-Slade Hallucination Scale Revised – LSH-R	A revision of the original 1981 scale to include a Likert-type response format. Also, the two negative response items in the original scale were made into positive response items. 12 items.	5-point Likert scale	Bentall and Slade, 1985
Rust Inventory of Schizotypal Cognitions - RISC	A 26-item measure of cognitive traits qualitatively associated with the positive symptoms of schizophrenia.	4-point Likert	Rust, 1988
A scale for the measurement of Schizotypy	A 30-item measurement of sub-dimensions of positive schizotypy (cognitive, perceptual and attentional function) and negative schizotypy (social dysfunction, social anhedonia, and physical anhedonia).	True/False	Venables, Wilkins, Mitchell, Raine, and Bailes, 1990

Oxford-Liverpool Inventory of Feelings and Experiences – OLIFE	A 150 item, multi-dimensional schizotypy questionnaire measuring the following four constructs of schizotypy: unusual experiences, cognitive disorganization, impulsive nonconformity and introverted anhedonia.	Yes/No	Mason, Claridge, and Jackson, 1995
The Barratt Impulsiveness Scale – BIS II	A 30-item questionnaire measuring attentional and cognitive impulsivity.	4-point Likert scale	Patton, Stanford, and Barratt, 1995
Referential Thinking Scale - REFS	A 34-item questionnairedesigned to measure the tendency to ascribe personal meaning to neutral, everyday occurrences.	True/False	Lenzenweger, Bennett, and Lilenfeld, 1997
Peters Delusions Inventory - PDI	A 40-item inventory measuring delusional ideation- the tendency to hold on to false beliefs despite strong contravening evidence.	Yes/No followed by three rating scales (1-4) for “yes” responses. providing a measure of distress, preoccupation, and conviction	Peters, Joseph and Garety, 1999

Revised Launay Slade Hallucination Scale	A 15-item version of the original 1981 scale, revised to include items associated with visual as well as auditory hallucination-like experiences such as vivid imagery and daydreams.	4-point Likert scale	Morrison, Wells, and Nothard, 2000
Schizotypal Ambivalence Scale	A 19-item revised version of the Intense Ambivalence Scale.	True/False	Kwapil, Mann, and Raulin, 2002
Revised version of the Launay-Slade Hallucination Scale	Adaptation of the original 1981 scale to include items referring to tactile and olfactory hallucinatory experiences. 16 items.	5-point Likert	Larøi, Marczewski, & Van der, Linden, 2004
Thinking and Perceptual Style Questionnaire	A 99 item questionnaire measuring 9 subscales of schizotypy, namely: physical anhedonia, social anhedonia, hallucination proneness, social paranoia, negative evaluation, thought disorder, magical ideation, self-referential ideation, and perceptual illusion.	5-point Likert	Linscott and Knight, 2004

The 21-item Peters Delusions Inventory – PDI-21	A brief version of the original 44-item PDI.	Yes/No followed by three rating scales (scored 1-4) for distress, preoccupation, and conviction for any endorsed items	Peters, Joseph, Day, and Garety, 2004
The Cardiff Anomalous Perceptions Scale - CAPS	A 32-item questionnaire measuring the intrusiveness and frequency of anomalous experiences.	Yes/No plus 5-point Likert ratings for distress, intrusiveness, and frequency for any “yes” responses given	Bell, Halligan, and Ellis, 2006
Schizotypic Syndrome Questionnaire - SSQ	108-item inventory assessing the following three subscales: negative, asocial and positive schizotypy.	4-point Likert	Van Kampen, 2006
Schizotypal Symptoms Inventory - SSI	A 20-item measure of sub-threshold psychotic symptoms.	5-point Likert	Hodgekins, Coker, Freeman, Ray-Glover, Bebbington, Garety, *et al*., 2012

Table 1. Questionnaires commonly used to measure individual differences in schizotypy. An adapted and expanded version of the table presented in Fonseca-Pedrero *et al*., 2008, p.580.

A key advantage of schizotypy research is that it allows researchers to study the cognitive processes associated with psychosis while avoiding some of the well-documented methodological issues associated with working with individuals with schizophrenia such as confounding effects of medication, extended periods of hospitalisation, low motivation, poor concentration, generalised neuropsychological deterioration, severe psychopathology, and comorbid alcohol and substance abuse. In addition, schizotypy research allows for the assessment of those unusual thoughts and behaviours that commonly precede an episode of psychosis (Poreh, Whitman, Weber & Ross, 1994) and which therefore have important implications for preventative and early intervention treatments (see McGorry *et al*., 2002; van't Wout, Aleman, Kessels *et al*., 2004).

Given the advantages and the potential usefulness of research with non-clinical participants discussed above, it might be informative to address some of the research questions in the schizophrenia and emotion processing literature, that have thus far produced inconsistent results, using non-clinical schizotypy samples instead. For example, how do high and low schizotypes vary in terms of emotion processing accuracy? Are errors of misperception in emotion processing affected by general schizotypy / specific schizotypy trait profiles? Addressing the latter question, for example, may help in our understanding of those types of errors that are frequently made by individuals with psychosis because data collected from clinical groups are usually noisy with effects of many of the confounding variables mentioned above. As such, research with schizotypy samples may provide a cleaner measure of the impairments apparent in clinical groups. A better understanding of misperceptions and errors of facial emotion processing in those with liability for schizophrenia would prove invaluable to the design of therapeutic interventions and remediation training aimed at reducing these errors in social situations, hopefully eventually leading to marked improvements in social functioning in individuals with psychosis. Where specific misperceptions (e.g., a tendency to frequently misperceive neutral faces as angry) may play a role in maintaining clinical symptoms or high arousal (a state that has been shown to predict the onset of positive symptoms of schizophrenia), then carefully designed interventions could also lead to symptom amelioration.

Another area of face and emotion processing in which individuals with schizophrenia deviate from the general population is in terms of laterality biases when viewing faces. Healthy individuals show reliable right hemisphere (left visual field) dominance for face and emotion processing (see Hole & Bourne, 2010) whereas patients with schizophrenia have been found to display a significantly reduced or completely absent hemifield bias during face processing (see Kucharska-Pietura, David, Dropko and Klimkowski, 2002). For example, using eye tracking techniques Phillips and David (1997) found that when images of faces were presented centrally onscreen, healthy controls tended to direct initial saccades to the left visual field (consistent with the right hemisphere dominance for face processing in the general population) whereas the schizophrenia patients made significantly more initial saccades to the right side of the face stimuli (indicative of left rather than right hemisphere dominance). Continuum models of schizophrenia predict that atypical laterality biases during face processing similar to those observed in schizophrenia patients would also be apparent in high schizotypes. There is, however, evidence to the contrary- Leonards and Mohr (2009), in a very similar experiment to the Phillips and David (1997) study, found that high schizotypes as compared to low schizotypal controls had significantly greater leftward biases in initial saccades to faces. Given that this was the first demonstration of a somewhat unexpected result, more research in this area would help to resolve this apparent contradiction. The third paper in this thesis therefore presents an attempt to replicate and extend the Leonards and Mohr (2009) finding.

In addition to atypical face processing in psychosis, it is well documented that individuals with schizophrenia also have disturbances in time perception (which, like the emotion processing impairment, may also be linked to a fundamental deficit in attentional processes), but the precise nature of the deficit is not fully understood (see Bonnot *et al*., 2011; Allman & Meck, 2012 for reviews). Discrepancy in the literature surrounding the nature of time processing deficits associated with schizophrenia may be the result of confounding effects of medication, generally small sample sizes and the very different methodologies used to assess temporal processing across these experiments (e.g., Bonnot *et al*., 2011; Davalos, Rojas & Tregellas, 2011). As previously discussed in this general introduction section, schizotypy research allows some of these issues to be circumvented and interestingly, there is some evidence that high as compared to low schizotypy is also associated with less accurate time perception (e.g., Lee *et al*., 2006). Importantly, there is potential for dysfunctions in face processing and time processing to interact. It has been shown, for example, that high relative to low anxious participants, overestimate the duration that an angry as compared to a neutral face is presented for (so for high anxious participants time appears to slow down when viewing angry faces) (Bar-Haim, Kerem, Lamy & Zakay, 2009). Given that individuals with schizophrenia and high schizotypes are particularly sensitive or hypervigilant to threat-related faces (see Green and Phillips, 2004 for a review), the interaction between time processing and exposure to emotional faces in the context of schizotypy is potentially very interesting, particularly in terms of how the subjective experience of exposure to threat may be moderated by schizotypy. It is possible that, for example, high schizotypes feel as though they were exposed to threat for longer than they in fact have been and that such an experience could serve to maintain a state of hypersensitivity to threat or even to maintain specific symptoms such as paranoia or anxiety. The association between time and emotion processing in the context of schizotytpy has not been previously researched and the final paper in this thesis presents a timely attempt at elucidating this important relationship.

This thesis presents a series of studies that explore the limits of optimal facial emotion processing in healthy individuals, and how facial emotion processing ability is related to individual differences in schizotypal personality traits. Four key themes are addressed: 1) the limits of healthy individuals' ability to rapidly attend to briefly presented nonfoveal faces, 2) the association between individual differences in schizotypy and misperceptions during facial emotion processing, 3) the relationship between laterality biases in face processing and schizotypy, and finally 4) the effects of schizotypy on facial emotion processing and time perception. Each of these themes is discussed in turn in the proceeding sections.

1. Evidence for preferential and rapid processing of emotional faces

1.1 The processing of faces as compared to other visual stimuli

As argued in the previous section, faces are central to everyday social experience. It is therefore unsurprising that humans appear to be particularly responsive to face as compared to non-face stimuli. Eye tracking studies provide evidence that upright faces are processed significantly more quickly than other animate stimuli such as inverted faces or butterflies (Crouzet, Kirchner & Thorpe, 2010). Furthermore, face stimuli, as compared to images of other animate objects matched for low-level visual properties, are particularly effective at capturing visual attention even when they are task irrelevant. For example, Devue, Belopolsky and Theeuwes (2012) presented a circular array of 6 dots. A task irrelevant image was positioned next to each dot in the array. On each trial one of these images was of an animate object (either an upright face, inverted face or a butterfly) and the remaining 5 images were of inanimate objects (e.g., a musical instrument, item of clothing etc.). One of the dots (the target) was always a different colour to the other five dots. Saccades to the target dot were significantly faster when its position was congruent with the upright face as compared to when the target dot was congruent with the inverted face or butterfly. Further, there were significantly more capture errors to upright faces than to inverted faces or butterflies when positioned at a non-target location (i.e., participants would mistakenly look towards the non-target dot positioned next to the upright face more frequently than to non-target dots co-located with inverted faces or butterflies).

Morand, Grosbras, Caldara, and Harvey (2010) asked participants to make a rapid eye movement either towards (prosaccade) or away from (antisaccade) images presented to the left or right of a central fixation cross. These saccade target images depicted faces, vehicles or noise patterns. Significantly more errors were made when individuals were required to saccade away from faces as compared to both cars and noise patterns, indicating that faces are particularly effective at capturing attention. Interestingly on the prosaccade trials, saccades were significantly faster to both faces and cars as compared to noise patterns (with no speed advantage for faces over cars). This may reflect the face-like appearance of the front of cars with, for example, headlights and number plates / grills corresponding to the position of eyes and mouth respectively. There is indeed further evidence that face-like stimuli are processed more rapidly than stimuli matched for low-level visual properties, but that are without a face-like appearance / configuration. Tomalski, Csibra, and Johnson (2009) presented oval shapes for 200 ms either to the left or right of a central fixation cross and participants were asked to look towards the stimulus as quickly as possible. The ovals always contained 3 small squares that either corresponded to the positions of the eyes and mouth on an upright face or of an inverted face. When schematic “upright faces” were presented, saccade latencies were significantly faster than when schematic “inverted faces” were presented (162 ms vs. 173 ms).

1.2 Rapid emotion discrimination

Faces are carriers of a wealth of important social information such as the identity, emotions and intentions of others. Our ability to accurately interpret the facial expressions of others is central to social functioning, and the rapid detection of threat-related emotion has important implications for our safety and survival. Given the importance of emotion processing to survival and social being, it is unsurprising that the intact human brain has evolved to be able to identify and discriminate between emotions extremely effectively. Electrophysiological measures of brain activity have revealed that the brain rapidly reacts in an emotion-specific way to facial expressions and emotional scenes. For example, Ashley, Vuilleumier & Swick (2004) recorded event related potentials to presentations of faces depicting different emotions (happy, fearful, disgusted, neutral) and found that in less than 250 ms there was a significant increase in P200 amplitude (as measured from electrodes placed around the frontocentral region) during the presentation of upright fearful faces as compared to faces expressing happiness and to non-face stimuli (houses).

The findings of a number of studies imply that the human brain is capable of processing emotional stimuli “pre-attentively” (see Dolan, 2002; LeDoux, 2000; Ohman *et al*., 2007). Information is said to have been processed pre-attentively when a participant displays behavioural or physiological changes resulting from their exposure to a visual stimulus that they explicitly report not having seen (Pessoa, 2005), or that they have not yet selected for visual processing (Wolfe, 2003). Preattentive effects can be studied using backward visual masking, which involves replacing the original stimulus with a masking stimulus (e.g., a grid pattern) at the exact time at which the researcher wishes processing of the original stimulus to terminate (Coltheart, 1980). Another method for assessing whether a stimulus has a “preattentive” effect involves measuring whether the presentation of a stimulus to non-foveal locations results in any measurable change in behaviour even though the stimulus has not been overtly attended.

Tamietto and de Gelder (2008) report that a fearful facial expression flashed centrally onscreen for 20 ms (so briefly that participants report not seeing a face) speeds up the recognition of a simultaneously presented fearful expression and slows down the recognition of a simultaneously presented happy expression. In other words, they claim to have found evidence for an effect of subliminal emotion processing on the conscious recognition of facial expressions. In addition, it has been found that these subliminal effects can vary by emotion. Whalen, Rauch, Etcoff, McInerney, Lee, & Jenike, (1998) investigated the difference in amygdala activity during the subliminal (33 ms) presentation of masked fearful and masked happy faces. They found that activation in the amygdala was significantly higher for subliminally presented fearful than happy faces and suggest that subcortical processing of emotional material may be limited to threat-related information.

Despite the evidence presented thus far in section 1 that faces are processed rapidly and preferentially, and the evidence above that facial emotions can even be detected preattentively, the limits and extent of this ability remain unknown. For example, it has not been established how far into peripheral vision we are able to distinguish emotional from non-emotional faces and whether these limits are systematically affected by facial emotion. In addition, it is generally agreed that attention is preferentially allocated to threat-related facial emotion and that there is obvious adaptive value in being able to rapidly and preferentially attend to threat-related emotional material (see section 1.3 below). It is unclear, however, what the limits of our ability to preferentially encode and respond to threat-related faces are, especially when these stimuli are located in extreme, nonfoveated peripheral locations. In other words, are the maximum non-foveated distal eccentricities at which we can identify facial expressions greater for threat-related faces than for non-threat related faces, as a result of the adaptive value of being able to swiftly recognise impending threats in the environment? Do the same mechanisms underlie both our ability to rapidly discriminate emotional versus unemotional natural scenes and our ability to discriminate emotional and unemotional faces even though the visual differences between emotional and neutral faces are considerably more subtle than the differences between two scenes varying in affective valence? The first paper in this thesis sets out to address some of these issues.

1.3 Preferential processing of threat-related faces

Researchers from a number of disciplines have studied the interface between threat-related information and attention in the human brain (see Compton, 2003; and for a review of neuroimaging studies in particular, see Davis & Whalen, 2001). Facial expressions of fear and anger, unlike the other basic emotions, convey information about impending danger. An angry face is threatening in itself and a fearful face indicates that a potential threat has been detected in the vicinity by someone else (Gerritsen *et al*., 2008). Ohman and Mineka (2001) among others propose that the heightened response to threat occurs because humans possess a highly evolved neural and behavioural module for facilitating a very rapid, defensive response to impending danger. LeDoux (1996) further states that fear functions to expedite a defensive response to survival threats. Indeed, a number of psychophysiological responses to threat-related experimental stimuli have been recorded, including increased muscle tone and heart rate (Palomba, Sarlo, Angrilli *et al*., 2000).

Whalen, Rauch, Etcoff, *et al*. (1998) investigated, using fMRI, the difference in amygdala activation (blood oxygen level-dependent (BOLD) fMRI signal) during the subliminal (33 ms) presentation of masked fearful and masked happy faces. Heightened activity in the amygdala during exposure to subliminally presented faces has been taken as evidence for involvement of the amygdala in the processing of the subliminal stimulus. Activation in the amygdala was significantly higher during the presentation of masked fearful faces as compared to masked happy faces. Evidence for subliminal processing of threat-relevant faces is, however, equivocal. Phillips, Williams, Heining *et al*. (2004), presented faces depicting fear subliminally (30 ms backward masked) to healthy participants. fMRI recordings did not reveal amygdala activation above baseline during the covert presentations of fearful faces. Heightened amygdala activation was only observed during exposure to supraliminally (170 ms) presented fearful faces.

Visual search experiments have also been used to explore whether threat-related as compared to non-threatening faces capture attention preferentially. In visual search tasks, participants are presented with a set of items (a search array) and are asked to search for a specific target item (which is typically only present on a subset of trials) within that array (Wolfe, 1998). The key measure is the time taken to decide whether the target is present or absent. Ohman, Flykt & Esteves (2001) found that fear-relevant stimuli were detected more rapidly than fear-irrelevant stimuli in visual search tasks. Interestingly, their experimental design allowed them to distinguish a specific “threat advantage” in visual search from a more general negative valence advantage. Participants reliably detected threatening (angry) faces more rapidly and more accurately than other faces with negative valence (e.g. scheming). Similarly, Fox *et al*. (2000) presented a search array consisting of schematic faces and asked participants to ascertain whether all the faces in the array were identical or whether one of the faces was different (i.e., depicting another expression). In target absent trials (all faces identical), participants were slower to complete the trial when the search arrays were made up of angry faces than when the arrays were made up of happy faces. In addition, target (discrepant) faces were identified more rapidly when they were angry faces than when they were happy faces. It appears then that angry faces are processed preferentially as compared to happy (or non-threat-relevant) emotional faces.

Further support for an attentional bias towards threat-relevant stimuli comes from experiments using the dot probe paradigm. Bannerman, Milders, de Gelder & Sahraie (2009) presented fearful and neutral faces simultaneously, and found that response times to a subsequently presented target dot were faster if the dot appeared where the fearful face was previously located compared to when it appeared where the neutral face had been located. They suggest that attention is preferentially allocated to the location of the threat-relevant stimuli and it therefore takes longer to disengage attention from this region in order to react to the appearance of a dot at a location other than where the threat-relevant stimulus was previously positioned.

1.4 The processing of emotional stimuli at varying distal eccentricities

As discussed more briefly in the general introduction, the concentration of receptors in the retina is not uniform, and as a result visual acuity is not constant across our entire visual field. By far the greatest concentration of cones (the photoreceptors responsible for colour vision that function in daylight conditions) is contained in the comparatively small foveal region of the retina. In an adult human this foveal depression measures a mere 650–700 μm in diameter (Yuodelis & Hendrickson, 1986), and is capable of resolving approximately two degrees of visual angle with very high acuity. There are far fewer cones in the surrounding parafoveal region (which corresponds to 2-10 degrees of visual angle) and virtually none at all in the peripheral retina, which is dominated by rods capable of detecting changes in luminance or motion that occur in the remainder of the visual field (which can be anything up to 200 degrees of visual angle for binocular vision) (Wade & Swanston, 2001). Around 80 percent of retinal ganglion cells (the axons of which form the optic nerve) in primates receive information from these foveal cones (Wade & Swanston, 2001). Since the optic tract axons (stemming from the optic nerve) terminate in the lateral geniculate nucleus (whose cells project to the primary visual cortex), a correspondingly large proportion of the cells in V1 process information from the foveal region (Wade & Swanston, 2001). As a result, visual acuity is greatest for the comparatively small region of the visual field that falls on the fovea and diminishes sharply with increasing distal eccentricity from the fovea.

We make two to three saccades per second in order to focus on those regions of the visual scene that contain the most salient or useful information given our current behavioural goals (Wade & Swanston, 2001). It is generally assumed that a saccadic eye movement to a specific spatial location is preceded by a covert (without moving the eyes) shift of attention to this region in space (Posner, 1980; Hoffman, 1998). Saccades are interspersed with fixations, during which the image on the retina is sufficiently still to be processed. Whilst there are different theoretical accounts of the relationship between attention and eye movements, it is generally agreed that they are closely linked (see Deubel & Schneider 1996, cf Rizzolatti, Riggio, Dascola, & Umilta, 1987; and see Hutton 2008 for a review) such that the location and duration of fixations within a scene are typically assumed to reveal which aspects of the scene have been attended.

The factors that determine where we allocate our attention is a topic of considerable debate (see Burnham, 2007 for a review). Purely bottom up models of visual processing propose that attention is attracted to points of high salience in terms of colour intensity, contrast, orientation and so forth (Itti & Koch, 2001). Others argue that it is predominantly top down processes such as task instructions, expectancy or target descriptions that affect the location and order of saccades during visual processing (e.g., Yarbus, 1967; Wolfe, Cave & Franzel, 1989; Zelinsky, Zhang, Yu, Chen & Samaras, 2006). More recent theories generally argue for some combination of the two influences. Theeuwes (2010), for example, contends that the allocation of visual attention is initially stimulus driven (bottom up), but with time top-down effects also begin to influence which aspects of the scene are selected for processing.

What is particularly interesting about the effect of bottom up influence is that the information that is used to guide subsequent saccades is extracted from non-foveal regions where visual acuity is comparatively diminished. As mentioned, the limits of our capacity to draw upon important stimulus information such as emotional content located at extreme distal eccentricities is not yet fully understood. Only a few studies have sought to determine the extent to which threat-related stimuli are processed when such stimuli are located at different peripheral eccentricities. Calvo and Esteves (2005) presented faces foveally (within 2˚ of central fixation point) or parafoveally (between 2.1˚ and 5˚ of central fixation) for between 25 ms and 75 ms. Faces were then masked and a probe (face or word label) was presented. Participants were required to indicate whether the probe face depicted the same expression as the prime face or not. When the probe stimulus was a word (angry, happy, fearful or neutral), participants had to indicate whether the probe word described the expression depicted by the prime face or not. Results indicated that emotional faces were identified more accurately than neutral faces both when the primes were presented foveally and when they appeared in extrafoveal locations.

There is also evidence (e.g., Nummenmaa *et al*., 2009) that complex task-irrelevant emotional scenes presented at 2.5 degrees distal eccentricity can reduce the latency of saccades to co-located cues (prosaccades are faster to emotional than to neutral scenes), but whether similar impact is observed at greater eccentricities has not been established. De Cesarei *et al*. (2009) observed systematic modulation of brain activity during exposure to scenes of varying valence presented as far as 8.2 degrees eccentricity and for only 24 ms. Similarly, using MEG imaging techniques to record evoked brain activity, Bayle *et al*. (2009) found increased right hemisphere amygdala activation in response to peripherally (8˚ from fixation) presented fearful faces compared to peripherally presented neutral faces within the first 80 ms of viewing. Although it is clear that modulation of brain activity occurs in response to peripherally presented emotional material, more studies are necessary in order to establish whether emotional information presented at such distances impacts on overt allocation of attention as well.

1.5 Paper 1 Summary

Paper 1 presents a series of three experiments designed to build on the previous research suggesting that emotional stimuli are very rapidly and preferentially processed, and to address some of the issues and uncertainties raised in the previous section. Specifically, we set out to determine the limits of our ability to rapidly direct overt attention towards non-foveally presented emotional faces using a prosaccade task in which the face stimuli were presented at varying horizontal distances from a central fixation cross. Whether or not the presence of faces depicting varying emotions systematically affects rapid eye movements to a co-located cue was monitored. In addition, since a previous study used a similar prosaccade task to explore rapid discrimination of emotional content using natural scenes (Nummenmaa *et al*., 2009), this set of experiments allowed us to draw direct comparisons between our ability to rapidly discriminate emotionally charged scenes from neutral scenes with our ability to rapidly discriminate emotive from unemotional faces.

Task-irrelevant emotional (happy, angry and fearful) and neutral faces were co-located with two potential saccade targets positioned up to 12 degrees to the left and right of a central fixation cross. On each trial one face was emotional and the other was neutral. On half of the trials the cued saccade target contained the emotional face. The presence of emotional but not neutral faces at the location of the cued saccade target significantly reduced saccade latencies. This speeding effect was observed when the faces appeared in the potential target areas 150 ms before the cue appeared and when the cue and faces appeared simultaneously. The paper extends the literature in this area by highlighting that emotional faces (even when irrelevant to the experimental task) presented at extreme distal eccentricities can still be encoded and used to guide saccades, and that this process is an extremely rapid one, observable even with a 0 ms stimulus onset asynchrony. The ability to rapidly process emotional information from faces is fundamental to optimum social function. As discussed in the general introduction, many individuals present with sub-optimal emotion processing ability and schizophrenia is associated with particularly marked impairments in facial emotion processing. Continuum models of schizophrenia predict similar, though attenuated, impairment in high schizotypes. In the second paper, rapid processing of non-foveally presented emotional faces is explored in the context of schizotypy.

2. Misreading non-foveally presented emotional faces: the role of individual differences in schizotypy

Deficits in facial affect recognition are associated with a number of psychological disorders such as depression and bipolar disorder, but as with other cognitive deficits associated with psychopathology, the impairment is arguably most severe in schizophrenia (see Addington & Addington, 1988; Gaebel and Wolwer, 1992). Impaired facial emotion processing has long been associated with schizophrenia (see Edwards *et al*., 2002; Mandal *et al*., 1998; Morrison *et al*., 1988 for reviews) and impaired social functioning in schizophrenia is one of the most severe and enduring symptoms (see Mueser, Doonan, Penn *et al*., 1996 for a review). Converging research suggests that social cognition in schizophrenia is a strong predictor of functional outcome (see Hooker & Park, 2002; Kee *et al*., 2003 and see Couture, Penn, Roberts, 2006 for a review) and gaining a more thorough understanding of the cognitive deficits behind impaired emotion processing is imperative if we are to inform remediation strategies and develop treatments focussed on improving emotion processing ability and in turn social functioning.

2.1 Visual processing of emotional stimuli in individuals with schizophrenia

Bleuler (1911) provided one of the very first descriptions of impaired facial emotion processing in schizophrenia, and a large body of literature has since then attempted to uncover the precise nature of this deficit (see Mandal, Pandey, & Prasad, 1998 for a review). Researchers have been interested, for example, in whether the face processing impairments apparent in schizophrenia reflect a more general cognitive deficit that extends to other complex stimuli as well (i.e., the impairment is perhaps not distinct for faces) (see Kerr & Neale, 1993 for a review). Williams, Loughland, Gordon, and Davidson (1999) argue that the observed face processing deficits in schizophrenia do not reflect generalised cognitive deficit, and patients with schizophrenia do not show the same impairment when processing other, carefully matched complex stimuli. In an eye tracking study, Williams *et al*. (1999) showed that individuals with schizophrenia as compared to non-psychiatric controls elicited comparatively restricted visual scanning techniques and poorer recognition memory for non-degraded face stimuli. In contrast, there was no difference in recognition memory or scanning behaviour for face stimuli that were degraded using a mosaic filter (which results in fine detail being filtered out). Williams *et al*. (1999) postulate that these findings support a specific deficit in face processing that is distinct from impairments processing other stimulus types. Williams *et al*. (1999) broadly compared schizophrenic patients with non-psychiatric controls without investigating possible effects of specific symptom profiles on visual scanning when viewing degraded and non-degraded faces. Given that a number of studies have in fact suggested that positive symptoms of schizophrenia may be associated with extended scanning of visual stimuli (see Gaebel *et al*., 1986, 1987), it would have been particularly informative if the symptom profiles of the patients in the Williams *et al*. (1999) study were considered (e.g., by comparing the scan paths of patients with predominantly positive symptoms, patients with predominantly negative symptoms and non-psychiatric controls).

Whether or not facial emotion processing deficits are differential (e.g., in affect recognition specifically) or reflect a more general impairment in processing information from faces that may detrimentally impact on other abilities such as age discrimination or familiar face recognition has also been explored. In support of a differential deficit, a number of studies have found that individuals with schizophrenia perform as well as controls on, for example, face recognition or age discrimination tests, but are impaired relative to controls in affect recognition (e.g., Cutting, 1981; Gooding & Tallent, 2002; Heimberg *et al*., 1992; Hooker & Park, 2002). In contrast, other studies report impairment in schizophrenia as compared to controls both in affect recognition tasks and control tasks that require the processing of non-emotional information such as identity or age from face stimuli (e.g., Archer *et al*., 1994; Kerr & Neale, 1993; Kohler, Bilker *et al*., 2000; Salem *et al*., 1996). As pointed out by a number of authors (e.g., Behere *et al*., 2011; Flack *et al*., 1997; Kohler *et al*., 2000), the discrepancy in the literature could be explained by methodological inconsistencies across studies such as not matching the experimental and control tasks for difficulty, failure to partial out effects of antipsychotic medication dosage, symptomatology differences in the clinical groups compared across studies, and the wide variation in the types of face stimuli used between studies.

Ekman argues that there are six basic emotions that have evolved for their adaptive value (Ekman, 1994) and that these six emotions (happiness, anger, surprise, fear, disgust and sadness) are universally recognisable from their corresponding facial expressions (Ekman & Friesen, 1971). Although there is evidence that deficient emotion processing in schizophrenia spans across all six basic emotions (Weniger *et al*., 2004), the deficit appears to be stronger for negative emotions such as fear, sadness, anger and disgust (e.g., Bellack *et al*., 1996; Edwards *et al*., 2001; Gaebel & Wolwer, 1992; Kline *et al*., 1992; Mandal *et al*., 1998; Schneider *et al*., 1995; Van't Wout *et al*., 2007; cf. Wolwer *et al*., 1996) and emotion-specific deficits appear to vary by schizophrenia subtype. For example, when patients with schizophrenia were asked to sort pictures of expressive faces into piles according to the emotion being expressed, those with paranoid symptoms were particularly impaired for sadness and fear as compared to controls (with residual symptoms of schizophrenia). Those with disorganised symptoms, in contrast, showed impairment across all six basic emotions relative to the control group even after partialling out antipsychotic dosage (Weniger, Lange *et al*., 2004). Poole *et al*. (2000) also found a negative correlation between schizophrenia patients' positive symptom severity (specifically disorganised thoughts) and affect recognition accuracy in an emotion processing task. Furthermore, there is some evidence that non-paranoid schizophrenics are more impaired in emotion detection than patients with paranoid symptoms (see Kline *et al*., 1992; Phillips *et al*., 1999). It appears then, that emotion processing impairment is systematically affected by specific sub-dimensions of positive schizophrenia. Specifically, disorganised symptoms seem to predict greater impairment than other positive sub-dimensions and those with non-paranoid symptoms are likely to present with worse emotion discrimination ability than those with paranoid symptoms.

Research into the relationship between negative symptoms of schizophrenia and emotion recognition ability is somewhat inconsistent. Some studies have found no relationship between negative symptoms of schizophrenia and emotion processing ability whereas others highlight specific sub-dimensions of negative schizophrenia as particularly related to emotion processing impairment. For example, scores on a picture sorting task, in which individuals with schizophrenia were asked to categorise images by the emotion being depicted, were unrelated to negative symptoms of schizophrenia (Weniger, Lange *et al*., 2004). Deficits in processing facial emotion are, according to other studies however, related to negative symptoms such as anergia (e.g., Mueser *et al*., 1996), affect flattening (Martin *et al*., 2005), and alogia (e.g., Kohler *et al*., 2000). There is also evidence that poorer performance on emotion processing tasks may be associated with overall negative symptom severity (e.g., Baudouin *et al*., 2002). As well as the association between emotion processing deficits and specific symptoms, symptom severity and neurocognitive performance are both positively correlated with emotion processing impairment (Kohler, Bilker *et al*., 2000, cf Kucharska-Pietura *et al*., 2005).

Although there is discrepancy in the literature surrounding the relationship between schizophrenia and emotion processing, there is quite convincing evidence that emotion processing can be systematically affected by particular symptom types. It is likely therefore, that discrepancy in the literature reflects the wide heterogeneity in the psychopathology of schizophrenia, underscoring the importance of carefully considering inclusion criteria in terms of individuals' specific symptoms. Further, when comparing across studies, the prevalent symptoms in particular samples need to be equated for comparisons to be valid and informative.

False positive errors in emotion recognition research indicate that an individual claims to have seen an emotion that in reality was not there (e.g., misattributing anger to what is actually a neutral face), and in a sense this type of misperception is analogous of visual hallucinations in which an individual sees something that does not really exist. The majority of the research on emotion processing in schizophrenia has focussed on accuracy scores in emotion recognition / discrimination tasks. However, a limited number of studies have also considered error patterns and from these it appears that patients with schizophrenia are more likely than controls to mistakenly perceive negative emotions such as disgust (Kohler *et al*., 2003), fearfulness or sadness (Tsoi *et al*., 2008). Whether, as is the case in accuracy measures of emotion processing, these misattribution errors are specifically related to certain sub symptoms of schizophrenia has received very little attention. Paranoid symptoms of schizophrenia have been associated with heightened sensitivity to threat-related stimuli (e.g., Davis and Gibson, 2000; Kline *et al*., 1992; Pinkham *et al*., 2011) suggesting that there may be good grounds for hypothesising that schizotypy is associated with an increased bias to perceive neutral faces as angry / fearful. There are very few studies that have set out specifically to explore whether certain sub-dimensions of schizophrenia are associated with particular misattribution errors during facial emotion identification. An exception is a study by Behere *et al*. (2011) in which facial emotion recognition in schizophrenia patients (with and without positive symptoms) and controls was tested using static and video face stimuli. Those with positive symptoms were significantly more likely than both the clinical and non-clinical controls to misattribute threat to non-threatening faces. This study, however, could have been improved by using alternative analyses that allow for effects of poor accuracy in identifying particular emotions to be separated from a tendency to falsely see emotion on neutral faces since impaired emotion recognition and a tendency to misattribute emotion to neutral faces may in fact be dissociable processes.

It would be interesting to consider more specifically the role of sub-dimensions of schizophrenia (rather than the quite broad distinction between presence of first rank symptoms or not), especially given some of the previously discussed studies looking at accuracy in emotion detection which suggest, for example, that those with paranoid symptoms are better at emotion detection as compared to those with non-paranoid symptoms (Kline *et al*., 1992; Phillips *et al*., 1999). More research is necessary to further elucidate the role of very specific sub-symptoms of schizophrenia in emotion recognition deficits and in misattribution error patterns. For example, do those individuals who experience visual hallucinations make more misattribution errors during facial emotion processing, and how do these individuals compare with those who experience non-visual hallucinations such as auditory or somatic hallucinations? The broader distinctions between positive and negative symptoms or between first rank or no first rank symptoms of schizophrenia are unable to answer these more detailed, specific questions around the cognitive mechanisms underlying both visual hallucinatory experiences and facial emotion processing deficits (in terms of accuracy and misperceptions). Subtypes of schizophrenia have also been associated with systematic differences in arousal ratings for expressive faces. In particular, disorganised symptoms predict higher overall arousal ratings (Wenige *et al*., 2004) and it has been speculated that this may be the result of increased intrusiveness (into working memory) of the emotional material in these individuals (Wenige *et al*., 2004).

It has been suggested that the emotion processing deficits evident in schizophrenia samples may result from atypical scan paths and sub-optimal allocation of attention when processing visual stimuli (Williams *et al*., 1999). In support of this contention, studies of face processing in schizophrenia using eye tracking techniques have revealed that individuals with schizophrenia, as compared to controls, free-view faces with shorter scan paths, fewer fixations and with reduced attention to the most salient or informative facial features (Loughland *et al*., 2002). In addition, the inefficient scanning of faces associated with schizophrenia persists across symptom dimensions of the disorder (Williams *et al*., 1999). Failure to attend to those facial features that provide the most information about another's emotional state would inevitably be detrimental to emotion recognition accuracy which would in turn be detrimental to social competence- the inability to accurately read the expression on another's face could lead to inappropriate social responses to others, for example.

To summarise, although there is convincing evidence for specific difficulties in processing facial emotion in schizophrenia, there are inconsistencies in the literature with regards to the role of specific sub-dimensions of schizophrenia and how these individually contribute to overall emotion processing impairment. Methodological issues such as variation in tasks and in stimuli used across experiments may offer partial explanation for the discrepancies in findings. The heterogeneous nature of schizophrenia psychopathology is also extremely likely to contribute significantly to some of the apparent divergence in the literature. This claim is not only supported by studies indicating that emotion processing deficits vary by sub-symptoms of schizophrenia, but also by neuroimaging experiments illustrating that neural responses to emotional stimuli vary significantly by schizophrenia subtype (Andreasen & Carpenter, 1993). Finally, a number of studies converge to suggest that the emotion processing deficits apparent in schizophrenics may be due to restricted visual scanning in which the most informative regions of faces are attended relatively infrequently.

2.2 Emotion processing and individual differences in schizotypy

It is currently unclear whether the marked emotion recognition deficits (Edwards *et al*., 2000) and sub-optimal allocation of attention to emotional material (Williams, Loughland, Gordon & Davidson, 1999) characteristic of patients with schizophrenia are also evident, but to a lesser extent, in sub-clinical schizophrenia groups such as in those with inflated schizotypy scores (as would be predicted by continuum models of psychosis). The literature on face processing and schizotypy is still very small, and the topic has certainly been considered far less than emotion processing in schizophrenia (see Phillips and Seidman, 2008 for a review).

There are a handful of studies that offer some support for the hypothesis of continuity between emotion processing disturbances in schizophrenia and schizotypy. Williams, Henry and Green (2007) for example presented one target face and seven comparison faces to high and low schizotypes, and asked participants to point out which of the comparison faces had the same expression as the target face. A wide range of target emotions were used (anger, fear, happiness, sadness, surprise, disgust and neutral). Individuals with inflated negative schizotypy scores on the Schizotypal Personality Questionnaire (Raine, 1991) made significantly more errors identifying negative emotions (anger, fear and disgust) even after controlling for group differences in general face processing using the Benton test of facial recognition (Benton *et al*., 1983) and in depression / anxiety scores using HADS (Snaith, 2003). No significant difference between high and low schizotypes emerged in the recognition of positive emotions and, as the authors point out, this may be a result of the relative ease with which positive as compared to negative emotions are identified (Williams *et al*., 2007). The experimental design resulted in twice as many negative emotion categories (anger, fear, sadness, disgust) than positive emotion categories (happy, surprise) arguably making it (after an initial distinction between positive and negative) comparatively easy to correctly identify the emotion depicted by faces expressing positive as compared to negative emotion. Also, although the authors report no association between emotion recognition and positive schizotypy, the specific error patterns made by participants were not deconstructed which, given the results of other studies, may also have been related to sub-scales of schizotypy (particularly positive schizotypy). For example, when asked to classify the emotion depicted by happy, angry, fearful and neutral faces, Van't Wout *et al*. (2004) found that those individuals who endorse questionnaire items referring to unusual perceptual experiences were more likely to misclassify happy faces as either angry or fearful.

A study by Germine and Hooker (2011) also found an association between schizotypy (SPQ-B scores) and facial emotion discrimination deficits. Pairs of faces were presented to participants in rapid sequence (500ms inter-stimulus interval) and participants were given 7 seconds to decide whether the two faces depicted the same emotion (in the emotion block) or were of the same person (in the identity block). Unlike in the previously mentioned Williams *et al*. (2007) study, in which only inflated negative (not inflated positive or disorganised) schizotypy scores, as measured using the SPQ (Raine, 1991), were associated with poorer emotion identification, their study revealed that all of the subscales of schizotypy measured (interpersonal, cognitive-perceptual and disorganised) were negatively correlated with accuracy on emotion discrimination even after controlling for general face processing ability (identity discrimination). This study therefore suggests that the emotion recognition difficulties found in high schizotypes cannot be fully accounted for by general face processing difficulties in those with high schizotypy scores.

Finally, a study by Poreh, Whitman, Weber & Ross (1994) found no difference between high and low schizotypes in emotion processing ability. Emotional and neutral faces were presented to the left or right visual fields using a tachistoscope. After controlling for scores on a general face recognition task, there was no difference between high and low schizoptypes in emotion recognition ability. The authors suggest that any observed difference in emotion recognition associated with schizotypy score may in fact reflect generalized attentional dysfunction or visual perception deficits in high schizotypes rather than poorer performance in emotion recognition per se.

In summary, there is some evidence that the emotion processing deficits apparent in schizophrenia can be observed to varying lesser degrees in high schizotypes, although not all studies demonstrate this. It is likely that the discrepancy in results arises from variation in stimuli and tasks (particularly in terms of difficulty) and through the use of a wide range of different schizotypy measures. Clearly, further research is necessary to fully elucidate whether the emotion recognition deficits apparent in schizophrenia, and more specifically the way that these have been shown to vary by different sub-dimensions of the disorder, are mirrored in high schizotypes. This requires studies that are designed to assess how emotion processing ability varies by specific sub-dimensions of schizotypy (e.g., hallucination proneness, disorganised thoughts etc.) rather than by overall schizotypy scores. Further, research aimed to specifically investigate error patterns during facial emotion recognition are lacking in the schizophrenia literature and are non-existent in the schizotypy literature. As argued previously, error patterns are particularly important to study as frequent misperception of faces, specifically falsely seeing negative emotions would inevitably have detrimental implications for an individual's sense of safety or of acceptance from others. Feeling under threat or disliked by others is extremely likely to negatively impact social functioning and psychological wellbeing whilst possibly increasing arousal or hypervigilance to environmental threat or potential harm from others. Importantly, for individuals with paranoid symptoms these types of false positive errors / misperceptions in interpreting non-threatening visual stimuli such as unemotional faces or neutral scenes as threatening, for example, could serve to maintain or to exacerbate their paranoid symptoms. In order to circumvent a number of the difficulties associated with clinical research (e.g., whether or not individuals are well enough to take part, confounding effects of medication, low motivation etc.), research in this area would benefit greatly from the use of non-clinical samples (e.g., by considering systematic effects of sub-dimensions of schizotypy on emotion recognition and error patterns during facial emotion processing). Experiments designed especially to assess error patterns in emotion recognition in schizotypy could be extremely informative to our understanding of impaired emotion processing in individuals with particular symptoms or sub-types of schizophrenia and it is clear that more studies are required to ascertain whether or not there is support for the hypothesis of continuity for error patterns in emotion processing.

2.3 Paper 2 Summary

The study presented in paper 2 was designed to assess the relationship between rapid emotion processing and schizotypy with particular interest in error patterns during emotion identification. Unlike previous emotion recognition studies, the experimental task used here was purposefully designed to generate false positive errors so that participants' misattribution error patterns (ascribing an emotion to a neutral face) could be analysed. Two faces were briefly presented onscreen either side of a central fixation cross and participants were asked to judge whether both faces were neutral in expression or whether one of the faces was emotive. The study allowed us to measure accuracy as well as misattribution error rate, so that effects of general poor performance in emotion recognition could be considered when assessing tolerance for false positives. This was achieved through signal detection theory from which sensitivity (accuracy) and response bias (tendency to make false positive errors) scores are derived for each participant. In light of research suggesting that hallucinations are the result of a perceptual system that has evolved to tolerate false positives during threat identification (Dodgson & Gordon, 2009), we set out to investigate whether more false positive errors (ascribing emotion to one of the faces presented in a neutral – neutral trial) occur when the target emotion is anger (angry block) than when the target is another less threatening emotion such as happiness or fear. To test continuum models of visual hallucinatory experiences, we also measured individual's hallucination proneness score to investigate whether error patterns vary as a function of susceptibility to visual hallucinations. Scores on questionnaires assessing general schizotypy and auditory hallucination proneness were treated as covariates.

High as compared to low hallucination proneness was associated with poorer emotion recognition across all emotion blocks (happy, angry and fearful), and with increased false positive errors in the angry block only. Our results provide evidence for poorer emotion recognition in high schizotypes (specifically those with susceptibility for visual hallucination) and therefore offer further support for continuum models of emotion identification deficits in schizophrenia / schizotypy. The fact that the high hallucination prone group was poorer at emotion identification for all emotions, but only made significantly more false positives than the low group in the angry block suggests that the tendency to misperceive neutral faces as angry cannot be explained by comparably poorer emotion identification by the high group- if this were the case, more false positives by the high hallucination prone group would have occurred equally across all emotion blocks. These results suggest that hallucinations are more likely to occur when individuals are hypervigilant to threat and support continuum models of positive symptoms of schizophrenia – specifically symptomatic visual hallucinations fall on a continuum with anomalous perceptual experiences in the general population.

Finally, all individuals were more accurate at emotion discrimination when emotional faces were presented to the left as compared to the right visual field (and thus processed predominantly by the right hemisphere). This result is consistent with a right hemisphere advantage for face / emotion processing (see section 3 for further discussion on laterality biases in face processing). There was also a trend for more misattributions of emotion to neutral faces that were presented to the right visual field, showing that laterality biases in facial emotion processing also extend to misattribution errors. A considerable body of literature suggests that hemispheric asymmetry in schizophrenia is anomalous with the general population, specifically that “normal” lateral asymmetry is attenuated or non-existent in schizophrenia patients. One manifestation of atypical lateral asymmetry is altered laterality biases during face processing in schizophrenia as compared to healthy controls. Specifically, the right hemisphere dominance for face processing in the general population is reportedly less apparent in schizophrenia patients. However, we did not find any interaction between schizoptypy and laterality (for accuracy or errors) in this study. Most reports of atypical laterality biases in schizophrenia use chimeric faces and are therefore interested in an effect of left versus right hemifield of the face stimuli on task performance (e.g. by asking participants whether the right or left side of a face looks more emotive). Here we presented two whole faces- one to the left visual field and one to the right which may explain why no interaction between schizotypy and laterality was observed. The proceeding study was designed specifically to investigate whether the attenuated (as compared to the general population) laterality biases during facial emotion processing in schizophrenia are also evident in healthy individuals with high schizotypy scores using a task that is more sensitive to laterality biases in schizophrenia.

3. Schizotypy and lateral asymmetry in facial emotion processing

3.1 Lateralised emotion processing

During saccades the image is not stable enough on the retina for us to “see”, so there is some cost involved when we decide to make a saccadic eye movement to a new location. A large degree of filtering occurs, therefore, as we sample the visual environment, and an inevitable consequence of this selectivity is that significant proportions of the visual field are not fixated (Tatler, Baddeley & Gilchrist, 2005). As such, patterns of saccadic eye movement to a given scene represent “decisions” about whether or not to fixate certain elements of the visual environment, and these decisions are influenced by a number of factors (for further discussion see Findlay & Gilchrist, 2003).

Due to the anatomical arrangement of the neural pathways from the eyes to the visual cortex, visual information presented to either the left or the right visual hemifield is received in the contralateral cerebral hemisphere (primary visual cortex) (Wade & Swanston, 2001) and there is an established link between hemispheric activation and contralateral eye movements (see Charlton, Bakan and Moretti, 1989). The location of fixations within a given scene, therefore, not only reveals which aspects of a scene are being selectively resolved in high acuity, but may also indicate which cerebral hemisphere is dominant in the selection and initial processing (information reaches the contralateral hemisphere first) of this visual information.

The two cerebral hemispheres in the human brain are functionally different and a number of cognitive (e.g., language and face recognition) and motor (e.g., handedness) functions are lateralised- preferentially carried out predominantly by the right or left cerebral hemisphere. It is unlikely that any function is carried out solely by one hemisphere in the healthy human brain given that the two hemispheres are linked by the corpus callosum (see Demaree *et al*., 2005 for a review), however, it appears that the direction and the degree of hemispheric specialisation varies between individuals (see Hellige, 1993). For example, even though fine motor control is frequently associated with left hemisphere specialization (the majority of the general population is right handed), there are still a number of individuals whose right hemispheres are dominant in fine motor control (e.g., approximately 8% of the general population is left handed), and as pointed out by Papousek and Schulter (2006), it is likely that individual differences in lateral asymmetries for other known lateralised behaviours also exist.

There is a large body of literature to support preferential involvement of the right cerebral hemisphere in face and emotion processing (see Adolphs, *et al*., 1996; Blonder *et al*., 1991; Borod, 1993; Ley and Bryden, 1979). Research with patients with focal brain damage, for example, reveals that impaired emotion recognition correlates significantly with lesions located in the right hemisphere (e.g., right inferior parietal cortex and right mesial anterior infracalcarine cortex), with emotion recognition unimpaired in individuals with lesions confined to the left hemisphere (Adolphs, *et al*., 1996). Another method for assessing hemispheric asymmetry in emotion processing involves hemifield tests which systematically manipulate visual information presented to the left and right visual fields. Bourne (2008), for example, presented on each trial two chimeric faces (in which one half of a vertically split face was neutral and the other emotional), one face above and one below a fixation point. One face in the pair always expressed emotion on the left whilst the other face in the pair always expressed emotion in the right chimera. On each trial participants were asked which of the two faces is the more emotive, and participants showed a significant bias towards choosing the face that depicted emotion in the left visual field, demonstrating an increase in sensitivity to emotional material that is processed predominantly by the right hemisphere.

The right hemisphere advantage for face and emotion processing is the result of “normal” cerebral asymmetry in the human brain. Schizophrenia, however, has long been associated with atypical lateral asymmetry and it has even been argued that this abnormal cerebral lateralization is central to the disorder (Crow, 1989). How atypical lateralization relates to differences in emotion processing between schizophrenia patients and controls is not yet fully understood, and it is to this topic that discussion will now turn.

3.2 Atypical hemispheric lateralization in schizophrenia

As discussed in section 3.1, schizophrenia has long been associated with atypical hemispheric lateralisation but the precise nature and cause of anomalous cerebral dominance in schizophrenia patients has not yet been fully elucidated (see Oertel-Knoechel and Linden, 2011; Shenton *et al*., 2001 for reviews). There is a significantly higher incidence of mixed hand preference in schizophrenia samples as compared to population estimates which implies that schizophrenia is associated with patterns of cerebral asymmetry anomalous with the general population (see Satz & Green, 1999 and Sommer *et al*., 2001 for reviews). In addition, it appears as though these cerebral differences are also apparent in young, early onset patients as well. Collinson, Phillips, James, Quested & Crow (2004) assessed whether lateral biases in hand and eye preference in an early-onset schizophrenia sample close to first episode (n=44) were anomalous with lateral preferences in the general population as they are shown to be in chronic schizophrenia samples. There was an increase in mixed handedness and a decrease in left eye dominance in their early onset sample as compared to estimates for the general population. Their study provides further support for atypical cerebral lateralisation characteristic of schizophrenia.

3.2.1 Schizophrenia and laterality biases in face processing

Laterality biases in face processing, another manifestation of cerebral asymmetry, are also deviant in schizophrenia as compared to the general population. In contrast to the left hemifield bias for face processing observed in the majority of healthy participants, patients with schizophrenia have been found to display a significantly reduced perceptual asymmetry or indeed no hemifield bias at all for facial emotions (Kucharska-Pietura, David, Dropko and Klimkowski, 2002). White, Maher and Manshreck (1998) presented faces or letters to either the right or to the left visual field (tachistoscopic presentation). For certain letters / faces the participants were required to make a manual response (go trials) and for other letter / face types participants were required to inhibit a response (no go trials). Unlike the controls who showed a performance advantage for faces presented to the left visual field (consistent with preferential processing of faces in the right hemisphere), patients showed no hemifield advantage during the face trials. Furthermore, David and Cutting (1990) asked patients with schizophrenia to decide whether happy-sad chimeric faces depicted a happy expression or a sad one. Unlike the controls, who showed the expected left-hemifield bias (i.e. were more likely to think the overall emotion of the face was congruent with the emotion depicted by the left hemiface), the schizophrenia group had no bias in either direction. Finally, when face stimuli are presented, laterality differences between healthy individuals and schizophrenia patients are observable from the very first saccade- Phillips and David (1997) presented greyscale neutral faces to individuals with schizophrenia and to controls and compared the location of initial saccades to the face stimuli between the two groups. Controls displayed a significant left visual field bias for the initial saccade (as expected given that face processing is reportedly a right hemisphere specialization), while the schizophrenia group made significantly more initial saccades to the right side of the face stimuli, suggesting atypical (reversed) hemispheric specialization in the clinical group.

3.3 Laterality effects and schizotypy

Numerous studies report that, consistent with schizophrenia samples, there is also a higher incidence of mixed handedness in high schizotypes as compared to estimates for the general population (Chapman & Chapman, 1987; Grimshaw, Yelle, Schoger, & Bright, 2008; Kelley, 2012; Poreh, 1994; Shaw, Claridge, & Clark, 2001). There is some inconsistency surrounding which particular dimensions of schizotypy are most associated with mixed handedness. For example, Grimshaw, Yelle, Schogar and Bright (2008) found that mixed hand preference predicted higher magical ideation score while Stefanis (2006) found that it was the disorganized sub-scale of schizotypy that was most associated with mixed handedness. Asai & Tanno (2009) found that overall higher schizotypy scores predict mixed handedness, but that the association was particularly strong for positive sub-dimensions of schizotypy. Thus whilst several studies reveal atypical handedness variations in high schizotypes that are consistent with the schizophrenia literature, more research is required in order to fully elucidate the relationship between hand preference and specific sub-dimensions of schizotypy. The schizotypy literature nevertheless offers support for the hypothesis of continuity between schizophrenia and schizotypy samples in terms of the atypical incidence of particular laterality biases manifesting themselves as left, right or mixed hand preference.

3.3.1 Schizotypy and laterality biases in face processing

As in the schizophrenia literature, manifestations of atypical laterality biases associated with high schizotypy also extend beyond hand preference to other typically lateralized abilities such as face processing. The left-hemifield (right hemisphere) bias when viewing chimeric faces has been shown to be attenuated in both individuals with schizophrenia and in those who have higher negative schizotypy (social anhedonia) scores (Luh and Gooding, 1999).

However, the direction of laterality biases in high schizotypes during face processing has been shown to diverge from those found in patients with schizophrenia. For example, Leonards and Mohr (2009) tracked participants' eye movements during free-viewing of face and fractal stimuli and found that elevated positive schizotypy (magical ideation) was in fact associated with an increased bias in initial saccade landing positions towards the left side of the face (i.e. indicative of greater right hemisphere involvement during face processing). This unexpected laterality finding is in direct contrast to the clinical group in the Phillips and David (1997) study who demonstrated increased saccades to the right and therefore comparatively greater left hemisphere preference.

3.4 Paper 3 Summary

The aim of paper 3 was to further investigate the association between schizotypy and lateral asymmetry in gaze behaviour during face processing given the apparent discrepancy with clinical studies. We speculated that some low-level stimulus characteristics that were not matched across the face and non-face stimuli used by Leonards and Mohr (2009) may have confounded the results. An alternative explanation for their finding, for example, could be that high schizotypes are more sensitive than low schizotypes to the visual differences (e.g. in colour or shape) between faces and fractals and that it is a visual characteristic of the face stimuli such as their smaller size (fractals were larger) or their shape (faces were oval whereas fractals were rectangular) rather than being the fact that they are faces per se that was driving the differences in gaze behaviour when viewing faces as compared to fractals. In order to rule out possible influence of bottom-up processes, we improved the experimental stimuli used in the original Leonards and Mohr (2009) study by matching the face and fractal stimulus sets for shape, size and colour, and by using symmetrical rather than asymmetrical fractals in order to make them more "face-like". With the improved stimuli, we attempted to replicate the somewhat unexpected finding that higher schizotypy scores are associated with an increase in leftward initial saccade and dwell bias when viewing faces but not when viewing fractals.

In support of the Leonards and Mohr finding, there was a significant positive association between Magical Ideation (MI) and extent of left side bias for initial saccade landing points and dwell times when free-viewing faces with the new, improved stimuli. Also consistent with the original study, there was no such association when viewing the fractals. We therefore provide further evidence that high schizotypes' laterality biases during face viewing are not in the same direction as schizophrenia patients'. We speculate that effects of medication on patients' performance may, in part, explain the apparent discrepancy. We also postulate that the patient sample in the Phillips and David (1997) study predominantly suffered delusions and negative symptoms, whereas the high schizotypes in our sample and in the Leonards and Mohr (2009) sample endorsed items referring to magical ideation - these two sub-dimensions are not qualitatively equivalent. We suggest future research explores the role of specific sub-dimensions of schizophrenia and schizotypy on face processing laterality biases.

As an extension of the Leonards and Mohr study, the emotion depicted by the faces was also manipulated in order to investigate whether laterality biases vary as a function of emotion. Previous research suggests that laterality biases are systematically affected by arousal (Alfano & Cimino, 2010) and given the findings of paper 2 that high schizotypes were hypersensitive to angry faces it was possible that the laterality biases of high schizotypes may have been particularly sensitive to exposure to anger. However, there was no overall effect of emotion, nor was there any interaction between schizotypy and emotion on laterality biases during face processing. Paper 2 in the thesis suggests that high schizotypy is associated with a hypervigilance to potential threat in the environment resulting in a higher tolerance for falsely perceiving threat when it is not in fact there. However, when really exposed to angry faces as was the case here in paper 3, there was no measurable difference in behaviour (gaze biases to the left or right hemiface) between high and low schizotypes. Laterality biases in gaze, however, tell us very little about an individual's subjective experience of exposure to certain stimuli. A left side bias for face processing is consistent with the general population yet most people are unaware that they more frequently look initially to one side of a face than to another. In order to assess whether different facial emotions systematically affect the subjective experience of being exposed to faces would require a very different task to simply free-viewing faces. One way to tap into variation in the experience of being exposed to, for example, threatening as compared to non-threatening faces, could be to measure an individual's perception of how long they were looking at the face for. It is possible that with a hypersensitivity to threat comes a tendency to overestimate exposure time- in other words some individuals may feel as though they are exposed to certain types of faces for longer. The final study in the thesis aims to explore whether an individual's subjective experience of time is systematically affected by both emotion and schizotypy.

4. Effects of schizotypy on time perception during exposure to emotional faces

An accurate perception of time is essential to daily living (Bonnot, 2011) and has important implications for the subjective experience of how long we have been exposed to certain types of stimuli (e.g. those related to reward or threat) for. Importantly, research suggests that time estimates are systematically affected by the presence of different facial expressions (Effron *et al*., 2006). Specifically, when individuals are exposed to threat-related faces time is frequently overestimated – people feel as though more time has passed than actually has (Droit-Volet *et al*., 2004; Droit-Volet & Gil., 2010). Importantly, time perception is altered in schizophrenia as compared to healthy individuals, but the research in this area is limited and has arguably been neglected in recent years (Bonnot, 2011).

A number of studies show that highly anxious people have attentional biases to angry faces- specifically they fixate threat-related stimuli such as angry faces for longer than controls in the initial 1800 ms of exposure (Rohner, 2002) and, unlike low anxious individuals, they experience difficulties disengaging visual attention from threatening faces (Georgiou *et al*., 2005; Yiend & Mathews, 2001). It is argued that this pattern of behaviour may serve to maintain their highly anxious state (see Fox, Russo & Dutton, 2002). Inaccurate time perception may indicate that a person feels as though they have been exposed to certain stimuli for longer or shorter periods than, in reality, they have been and this experience itself may also serve to moderate psychological states such as mood, anxiety and hypervigilance in the same way that increased dwell to threat, for example, likely serves to maintain states of anxiety. Whether inaccurate perception of time is involved in maintaining high arousal levels and a hypervigilance to threat-related stimuli, such as angry faces, in schizophrenics or high schizotypes has not previously been directly explored. Given that high arousal levels and hypervigilance in schizophrenia are related to positive symptoms of the disorder (see Corcoran *et al*., 2003), research in this area is fundamental. The final section of the thesis, therefore, aims to explore the nature of the interface between emotion processing and time perception and how this may vary as a function of positive schizotypy which requires, initially, an understanding of the dominant models of time processing in healthy individuals.

4.1. Models of time processing: the internal clock

According to internal clock models of time perception (e.g., Gibbon *et al*., 1984; Meck & Church, 1983; Wearden, 2004; Zakay & Block, 1996), humans possess an "internal clock" which consists of a pacemaker, a switch or gate (see Lejeune, 1998 for discussion), and a time pulse accumulator. As an event to be timed commences, the switch or gate closes and pulses emitted from the pacemaker begin to collect in the accumulator. At the cessation of the timed event, the switch or gate opens and no more pulses accumulate. Subjective time is based on the quantity of pulses that have been accumulated during the period being timed - duration estimates increase with the number of pulses collected. Heightened arousal is said to increase the speed of the pacemaker (Noulhiane *et al*., 2007; Zakay, Nitzan & Glicksohn, 1983) which results in the accumulation of more pulses over a given period (hence time would be overestimated). For example, time durations are consistently overestimated when individuals are exposed to arousing emotional (specifically angry and fearful), as compared to neutral faces during the “to be timed” interval (Droit-Volet *et al* 2004; Droit-Volet & Meck & Church, 2007; Schiff & Thayer, 1970; Tipples, 2008). In addition, stressful situations (in which arousal is increased) also result in the subjective slowing of time. For example, spider phobics overestimate the duration of the period that they were exposed to an image of a spider as compared to non-phobics (Watts and Sharrock, 1984). Furthermore, according to internal clock models, when attention is diverted away from timing the accumulation of pulses is disrupted and fewer pulses reach the accumulator (time is therefore underestimated). Dual-task experiments in which a secondary task is introduced to divert some attention away from the primary time processing task offer support for this contention because in such paradigms time periods are typically underestimated (Thomas and Weaver, 1975; Zakay, 1989).

4.2 Effects of emotional stimuli on time judgements

Experiments investigating time processing using affective stimuli such as expressive faces tend to support a predominant role of arousal rather than of attention on time processing during exposure to emotional material (e.g., Bar-Haim *et al*., 2010; Effron *et al*., 2006; Tipples, 2008; cf. Burle and Casini, 2001). Time estimates tend to be exaggerated when individuals are exposed to emotional as compared to neutral faces during the timing interval (e.g., Effron *et al*., 2006) when exposure durations are less than 4 s (Angrilli *et al*., 1997) and overestimations tend to be greatest for threat related emotions such as anger and fear in both adults (Droit-Volet *et al*., 2004; Droit-Volet & Gil., 2010) and in children (Gil, Niedenthal and Droit-Volet, 2007). Individual differences also play a role in time estimates during the viewing of affective stimuli. For example, higher negative emotionality (Tipples, 2008) and increased trait anxiety (Bar-Haim *et al*, 2010) both predict overestimations of time intervals, but interestingly effects of these individual differences are only evident in the most arousing experimental condition (trials that involve exposure to threat-related faces).

Paper 2 in the thesis provided evidence for oversensitivity to threat in high schizotypes (who were more likely than low schizotypes to misperceive neutral faces as threatening) which would suggest that these individuals may also be more likely than low schizotypes to overestimate the length of time that they are exposed to threat-related faces for. The experience of feeling exposed to threat in the environment for longer than controls has important implications for the maintenance of a sense of hypervigilance and for social functioning in schizotypy and schizophrenia and it is therefore surprising that time processing in schizotypy and, importantly how this relationship is affected by exposure to threat, has not previously been researched.

4.3 Time processing and the schizophrenia continuum

4.3.1 Time processing in schizophrenia

It is widely accepted that the ability to estimate time periods is altered in schizophrenia as compared to controls (e.g., Carroll *et al*., 2009; Elvevag, McCormack, Gilbert *et al*., 2003; Rammsayer, 1990; Tracy *et al*, 1998; Tysk, 1990; Volz *et al*., 2001), but the precise nature of any deficit has not been fully elucidated (Bonnot, 2011). It has been suggested that deficient temporal information processing in schizophrenia is related to, and may even underlie, some of the most intrusive symptoms and cognitive disturbances associated with the disorder (Andreassen, 1999; Volz *et al*, 2001) such as delusions of alien control, megalomania, and verbal auditory hallucinations. Specifically, it is argued that these experiences may be the phenomenological expression of dysfunctional neural timing (Carroll *et al*., 2009; Gallagher, 2000; Haggard *et al*., 2003; Shergill *et al*., 2005) and temporally disordered information processing (Bressler, 2003; Carroll, O'Donnell *et al*., 2009). Disturbances to an individual's sense of agency (e.g., the failure to recognise self-generated actions as your own, or the belief that one's own speech originated from an external source) are some examples of symptomatic behaviour in schizophrenia that have been argued to derive from disorderly temporal processing on a neural level (see Franck, Posada *et al*., 2005; Shergill, 2005). This argument is consistent with the contention that individuals with schizophrenia have difficulty forming a “specious present” from which they can think forward and backward in time (see Allman & Meck, 2012). Without this usual sense of the present, it is unsurprising that difficulties mapping self-generated actions to their corresponding consequences emerge in individuals with schizophrenia (see Franck *et al*., 2005).

Haggard *et al*. (2003) asked schizophrenia patients and matched controls to view onscreen a clock face with a revolving hand, similar to the second hand on a conventional clock (see Libet *et al*., 1983). One revolution lasted 2560 ms. Participants were asked to press a key at any point after they had viewed one full clock hand rotation. Following the key press there was a 250 ms delay before the “consequence” (an auditory tone) of their voluntary action occurred. At the end of each trial, participants were asked to verbally report the “time” (the position of the clock hand) when they had pressed the key, or to report when the tone sounded. In a second experiment a pair of auditory tones were played twice (with a 250 ms interval in between), and participants were asked to judge the time at which either the first or the second set of tones (depending on the trial) began to sound. For both experiments, the discrepancy between the perceived onset time of the event in question (key press / tone onset in experiment 1 or first / second tone sound in experiment 2) and the actual time that this event occurred was calculated. Participants consistently fused together action and consequence (e.g. the action was perceived to occur later and the consequence earlier than their actual onset times) but this occurred to a much greater extent in patients than controls. Importantly this “binding” of action and consequence was significantly more pronounced (twice as large) for patients in the first experiment which involved agency than in the second experiment which did not, implying that agency is highly involved in the observed “binding” effect. When the average perceptual shift in ms of the action towards its consequence and of the consequence towards the action that caused it in experiment 1 were considered for both groups, the patients judged the 250 ms delay between the voluntary key press and the onset of the tone as lasting only 51 ms (60 ms delay in action awareness and 139 ms anticipatory awareness of the consequent tone) in contrast to controls who judged the duration to be 229 ms.

Although binding experiments such as these imply a shortening of subjective time in patients as compared to controls, other types of temporal processing experiments (e.g., time production tasks) reveal a greater overestimation of the objective time period in patients as compared to controls. For example, Tracy *et al*. (1998) found that when asked to produce a specified time interval, schizophrenia patients overestimated whereas controls underestimated the given duration. Similarly, Wahl and Sieg (1980) report systematic overestimation of temporal durations by patients on a verbal time estimation task. However, not all studies of time perception in schizophrenia have reported overestimation. For example, Tysk (1983) and Penney, Meck, Roberts *et al*. (2005) both report an underestimation, whereas Carroll, O'Donnell *et al*. (2009) found no significant difference in time estimates. One possible explanation for discrepant findings is that a vast range of different paradigms are considered to tap into "temporal processing" (Davalos *et al*., 2011). For example, some tasks require visual processing during the timing intervals whereas others require auditory signals to be processed; different paradigms may require prospective or retrospective time estimates; the time intervals used across studies are not standardised; some tasks require voluntary action and others do not require agency. This last point is expanded by Haggard *et al*. (2003) who propose that tasks focussed on perception result in a lengthening of subjective time, whereas those requiring action have the opposite effect thus shortening subjective time estimates (see also Franck, Posada *et al*., 2005).

Individuals with schizophrenia display a number of behaviours that would suggest they might be particularly susceptible to arousal effects on time perception, and that the extent of these effects may depend on the nature of their positive symptoms. For example, Williams *et al*. (2004) found that individuals with paranoid schizophrenia displayed much higher skin conductance (a measure of arousal) to threat-related faces than did matched controls which might predict a greater arousal based “slowing” of subjective time in these individuals compared with matched controls. Similar heightened arousal responses to threat-related stimuli by schizophrenia patients have also been reported by, among others, Kring and Neale (1996). Heightened anxiety and arousal is not just predictive of altered time perception. Delespaul *et al*. (2002) report that state arousal and anxiety are particularly strong predictors of the occurrence and intensity of hallucination, again suggesting that there is an association between arousal, time processing, and positive symptoms of schizophrenia. Experiments designed specifically to assess how symptomatology, time processing and arousal interact are required if we are to fully understand the role of altered time processing in symptom exacerbation / maintenance, and importantly if we are to design interventions aimed at ameliorating the oversensitivity to threat and enduring sense of impending danger that many individuals with schizophrenia frequently experience.

4.3.2 Time processing and schizotypy

As argued previously, studies using non-clinical samples are potentially very informative in tapping into the cognitive mechanisms underlying altered time perception in schizophrenia not least because a number of confounds that pose problems for clinical studies can be avoided when non-clinical samples are used instead. However, no study has set out to explore how schizotypy is related to time processing during exposure to threat and non-threatening stimuli. One study, however, has more broadly considered time processing per se in schizophrenia using non-clinical samples- Lee *et al*. (2006) recorded time estimations by healthy students classified as high or low schizotypes (based on their scores on the Schizotypal Personality Questionnaire- SPQ) using a time bisection task in which participants were asked to categorise auditory tones lasting between 1000 ms and 2000 ms as closer to a probe short (1000 ms) or long (2000 ms) anchor duration. Bisection points (the tone duration giving rise to 50% "long" responses) were obtained for each participant. Analysis of bisection points revealed that high as compared to low SPQ scorers significantly underestimated the duration of the auditory tones. This underestimation of time by high SPQ scorers is consistent with findings from binding experiments, as previously discussed, in which individuals with schizophrenia tend to underestimate the intervening time between action and effect. However, it is unclear whether similar results would be obtained if the task focussed on the visual rather than on the auditory modality. In addition, since auditory tones were used in the Lee *et al*. (2006) study there was no scope to explore the influence of exposure to social threat on an individual's experience of time.

4.4 Paper 4 Summary

Following on from the established links between schizophrenia pathology (specifically positive symptoms), increased arousal and altered temporal information processing, and from the results of paper 2 in the thesis that reveal an oversensitivity to threat in high schizotypes, the aim of the final paper in the thesis was to explore the relationship between schizotypy and time processing and how exposure to social threat may moderate this relationship. Specifically, this last study was designed to investigate whether high positive as compared to low positive schizotypes present with altered time processing, and whether there is an interaction between schizotypy and exposure to threat on time processing such that the duration judgements made by the high schizotypes are particularly susceptible to alteration by threat exposure. This may provide another (as in paper 2 in the thesis) indication of oversensitivity to threat in high schizotypy, but this time highlighting how this oversensitivity to threat manifests itself in everyday experience (e.g., the subjective feeling of being exposed to threat in the environment may vary by schizotypy with some individuals feeling as though they are under threat for longer). In order to assess whether there is any effect of threat exposure on time perception, we manipulated the threat-relevance of the exposure stimuli by using happy, angry, fearful and neutral faces, with presentation of angry faces providing a condition in which participants are exposed to social threat. No other study to date has set out to investigate the relationship between schizotypy, time processing and exposure to social threat.

We used a time reproduction task in which, on each trial, participants viewed a happy, angry, fearful or neutral face for exposure durations of between 1 and 5 seconds. The face then disappeared and participants were asked to reproduce the time period that the face was present for with a spacebar press. Higher scores on a measure of hallucination proneness were associated with longer time estimates, but only during exposure to the angry faces. It appears then that when exposed to social threat, individuals susceptible to hallucinations feel exposed to the threat for longer than controls. It is argued that this experience itself may serve to maintain a state of hypervigilance which has been shown previously to be associated with positive symptoms of schizophrenia.

5. Conclusion

The thesis set out to explore the limits of facial emotion processing in healthy individuals, and how facial emotion processing is affected by individual differences in schizotypal personality traits. The literature on emotion processing deficits in schizophrenia is inconsistent and it was argued that this may reflect the fact that it is extremely difficult to obtain “clean” data from schizophrenia samples due to the many confounding variables associated with research with individuals affected by severe psychopathology. As argued in the general introduction section of the overview and elsewhere, there is a widespread consensus that a continuum of liability for schizophrenia exists, such that the disorder can be expressed in ways other than full-blown schizophrenia. The use of non-clinical samples varying in schizotypy, therefore, provides a valid means of testing the same liability, albeit attenuated and nonpsychotic that is at the root of schizophrenia psychopathology (Lenzenweger, 2010). Unlike research with schizophrenia patients, the data derived from schizotypy samples is not confounded by the effects of severe psychopathology and generalised neuropsychological deterioration, medication, hospitalization, low motivation and so forth.

The first section of the thesis focussed on the limits of healthy individuals' ability to accurately interpret facial emotion. This ability to correctly identify and appropriately respond to facial emotion is crucial for interpersonal communication and general social being, and our capacity to correctly interpret threat-related expressions has obvious adaptive value. Furthermore, in order to understand the mechanisms behind sub-optimal facial emotion processing it is useful to gain a thorough understanding of the maximum extent of intact facial emotion processing. Using eye tracking techniques to explore these limits, it was shown that the intact human brain is so specialised for facial emotion processing that it is possible to discriminate between nonfoveal emotional and neutral facial expressions so rapidly that this information can be used to selectively speed up prosaccades to the abrupt luminance changes that are co-located with emotional but not neutral faces. Furthermore, this happens even when the emotional face stimuli are task-irrelevant, located well into peripheral vision (where visual acuity is considerably compromised), and when the faces and the saccade cue appear simultaneously allowing no “extra” time to process the faces before saccade programming commences in response to the luminance change saccade cue.

These findings are consistent with Nummenmaa *et al*. (2009) who reported a facilitative effect of complex emotional but not neutral scenes on prosaccades. In contrast to the complex emotional and neutral scenes used in the Nummenmaa *et al*. (2009) study, the stimuli used here were very simple images of faces depicting emotional or neutral expression. The use of more simple emotional and neutral stimuli allowed for more careful control of the visual differences between stimuli falling with and between the different affect conditions because all faces share the same constituent parts regardless of expression whereas two scenes varying in emotional content are likely to be far more visually distinct. Despite the fact that, visually, the difference between an emotional and a neutral face is considerably more subtle than the difference between a positive/negative and a neutral natural scene, a facilitative effect on saccade latencies to emotional as compared to neutral faces was still observed. In addition, this facilitative effect of emotional as compared to neutral faces on prosaccades persisted even when the face stimuli were presented well into peripheral locations (at even greater distal eccentricities than in the Nummenmaa *et al*. (2009) study). Since the faces were presented nonfoveally, and the facilitative effect of emotional faces on prosaccades was apparent even with a 0 ms stimulus asynchrony between the presentation of the faces and the co-located cue, it was proposed that covert (without moving the eyes) shifts of attention towards the parafoveal emotional faces were driving the speeding effect on saccades towards emotional faces. This first paper presented in the thesis provides a timely demonstration that the ability to identify and respond to those very subtle differences between faces depicting different expressions is possible even when the faces are presented 12^0 to the left or right of fixation thus relying on information extracted from covert shifts of attention towards the faces. Interesting questions arise about exactly which aspects of the emotional faces were gleaned from these covert attention shifts and then used to speed up prosaccades to the co-located cue. Future research in this area could attempt to establish whether the facilitative effect of emotional faces relies on a crude representation of the entire face or a featural analysis of the face, extracting selective information from isolated face regions (e.g. those features with learned significance for emotion recognition). This could be achieved by presenting degraded and non-degraded faces as stimuli and assessing whether the same facilitative effect of emotional faces on prosaccades emerges when degraded face stimuli are presented (which would offer some support for a crude representation of the stimuli driving the facilitation). Furthermore, it would be interesting to see whether the same prosaccade facilitation is observed when isolated features of emotional versus neutral faces are presented as stimuli as opposed to whole faces. An example of this would be to just present the eyes or the mouth of fearful and neutral faces as stimuli- if specific elements of the faces are capturing covert attention and subsequently speeding up prosaccades to co-located cues, then the same speeding effect to emotional as compared to neutral features of faces might be observed for specific facial features and not for others. Studies like these would further elucidate the mechanisms underlying our highly evolved ability to respond to emotional faces.

There is certainly scope to improve the set of studies presented in the first paper of this thesis. Firstly, the error rates across the three experiments were low and as a result it was not possible to analyse error patterns. The experimental design could therefore be improved (perhaps with a less salient saccade cue, for example) so that the experiments generate a higher number of error saccades- analysing capture errors, for example, would be particularly interesting. Perhaps there were more error saccades to emotional faces when the cue was co-located with the neutral face in the pair, which would suggest that attention is drawn preferentially towards emotional faces even when completely task irrelevant and when competing against a task-relevant abrupt luminance change for visual attention. Additionally, the second study presented in paper 1 in this thesis only considered neutral and fearful faces since there was no evidence from experiment 1 that certain emotions exerted a greater influence on prosaccade latencies than others. However, it is possible that with the faces presented at greater distal eccentricities in the second study in paper 1, that some differences between emotions may have emerged. Recent research has found that the amygdala responds to the presentation of threat related stimuli presented outside of the focus of attention, and importantly, it is activated by low spatial frequency information (Vuilleumier, Armony, Driver and Dolan, 2003). The inclusion of emotional faces depicting expressions other than fear in the second experiment (in which the stimuli were presented up to 12^0 away from central fixation) may have revealed a greater congruency advantage for threat-related emotional (e.g. fearful or angry) over non-threat related emotional faces (e.g., happy or sad) at those most extreme locations.

Taken together, the findings from the set of experiments presented in paper 1 of this thesis support previous research that suggests facial affect can be processed extremely rapidly even when the faces are presented nonfoveally. The results presented in this paper were, however, the first demonstration that emotional faces presented 12 degrees peripherally can still exert influence on the very early stages of saccade programming- i.e., when there is no interval between the presentation of the face stimuli and the onset of the saccade cue.

The remaining studies explored the relationship between emotion processing accuracy and individual differences in schizotypy. Those who scored highly on measures of hallucination proneness were less accurate at identifying happy, angry and fearful faces and also more likely to misattribute anger to neutral faces. The finding that non-threatening faces were more frequently misperceived as angry by those with increased as compared to low liability for visual hallucinations supports previous research (e.g., Brown and Cohen, 2010) and is consistent with the predictions of continuum models of visual hallucinatory experiences. The finding was discussed in terms of “hypervigilance hallucinations”, a theory postulated by Dodgson and Gordon (2009) that contends that hallucinations may result from an over-tolerance for false positive errors during threat-detection.

This finding that high schizotypes are more likely than low schizotypes to falsely perceive threat on neutral faces suggests that these individuals are hypersensitive to threat in the environment. Therapeutic interventions aimed at increasing tolerance for potential threats in individuals with schizophrenia may prove to be effective in reducing the frequency and perhaps even the intensity (given that the theme of psychopathological hallucinations is often hostile- see Nayani and David, 1996) of symptomatic hallucinatory experiences. This study could be improved in a number of ways, including increasing the number of trials in each block and including a measure of handedness to control for those individuals with anomalous cerebral asymmetry (which would strengthen the analysis of lateral asymmetry in facial emotion misperception).

Given the results of this second paper, a further experiment was designed to assess differences in the subjective experience of exposure to threat in the environment between high and low schizotypes. This study revealed that higher hallucination proneness was associated with longer time estimates, but only during exposure to the angry faces during the exposure period. This study therefore provides further evidence that high as compared to low schizotypes are more hypersensitive to social threat – high schizotypes feel as though they have been exposed to angry faces for longer, an experience that possibly serves to maintain hypervigilance to social threat and that may even contribute to the increased tendency to falsely perceive threat (e.g., an angry face) in the environment. This finding implies that the effectiveness of therapeutic intervention aimed at ameliorating positive symptoms in schizophrenia may be improved with increased focus on reducing the hypersensitivity to threat that is associated with schizophrenia. In order to further elucidate the role of threat hypersensitivity in time overestimation, it would be interesting to assess whether initially desensitizing participants to the threatening face stimuli attenuates the overestimation of time in high as compared to low schizotypes. It would also be interesting to track participants' eye movements during this task to investigate whether high and low schizotypes vary systematically in terms of which facial features they predominantly dwell on during exposure to the face stimuli and whether increased dwell to or even avoidance of particular features (e.g., the eyes of angry faces) correlates with time overestimation.

Finally, given the inconsistency in the schizophrenia literature concerning laterality biases during face perception in schizophrenia and schizotypy a further study in this thesis attempted to elucidate the relationship between schizotypy and laterality biases during face processing. Contrary to the predictions of continuum models of schizophrenia, higher magical ideation score predicted a greater leftward bias for initial saccades and for dwell times to faces presented centrally onscreen. This finding was consistent with the first report by Leonards and Mohr (2009) of this unexpected directional bias. The finding is nevertheless contrary to continuum models of psychosis– a left-side bias for face processing is in agreement with the general population, whereas schizophrenia is associated with a rightward or indeed no bias for face viewing. More studies, considering a wider variety of schizotypy measures, are required to further understand the increased left-side bias observed in high schizotypes and how this relates to the schizophrenia literature. It was speculated that issues equating clinical and non-clinical samples across studies (in terms of appropriately matching schizotypal traits with their corresponding psychopathological symptoms or symptom profiles) combined with potential confounding effects of medication may, at least partially, explain the discrepancy. The study could therefore have been improved by using schizotypy measures more carefully matched to the original clinical study by Phillips and David (1997) reporting the increased rightward bias in initial saccades during face processing in individuals with schizophrenia.

There are some more general improvements / extensions that could be applied to all experiments presented in this thesis to strengthen the studies. Firstly, considering a broader range of schizotypy measures and how specific combinations / clusters of these scores interact to affect emotion processing ability across the range of tasks would help to elucidate whether emotion processing impairments in schizophrenia are linked with particular symptoms / symptom profiles and would provide a fuller understanding of the disorder. In addition, throughout the thesis it is assumed that the way that individuals process pictures of emotive faces in a laboratory setting is representative of how the same individual processes real faces in natural settings. It would be particularly interesting to replicate the studies with more ecologically valid face stimuli such as photographs of natural rather than posed expressions and video images of emotional expression rather than static images in order to ensure that any differences in emotion processing ability observed in laboratory settings have external validity. Perhaps, for example, the differences in emotion processing observed between high and low schizotypes are in part driven by the inherent unnaturalness of the posed face stimuli, and as a result the observed differences in emotion processing impairment across the schizophrenia spectrum may vary with the use of more natural stimuli.

In summary, the thesis set out to explore the relationship between individual differences in schizotypy and facial emotion processing. The series of papers presented offer partial support for the hypothesis of continuity between the impairments in emotion discrimination observed in individuals with schizophrenia, and normal, healthy variation in facial emotion processing. The main finding to emerge was that high as compared to low schizotypes are particularly hypervigilant to social threat, and that this state appears to manifest itself in an increased tendency to misattribute anger to emotionally neutral faces and to experience time as slowing down during exposure to angry faces. It has been argued in this thesis that these experiences may themselves serve to maintain symptoms such as paranoia and visual hallucinations in schizophrenia patients. Further research projects aimed at investigating whether interventions which target a reduction in threat hypervigilance result in improved emotion processing ability, and in turn social functioning, in individuals with schizophrenia are strongly encouraged.

6. References

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1. The influence of extrafoveal emotional faces on prosaccade latencies

1.1 Abstract

Across three experiments we sought to determine whether extrafoveally presented emotional faces are processed sufficiently rapidly to influence saccade programming. Two rectangular targets containing a neutral and an emotional face were presented either side of a central fixation cross. Participants made prosaccades towards an abrupt luminance change to the border of one of the rectangles. The faces appeared 150 ms before or simultaneously with the cue. Saccades were faster towards cued rectangles containing emotional compared to neutral faces even when the rectangles were positioned 12 degrees from the fixation cross. When faces were inverted, the facilitative effect of emotion only emerged in the -150 ms SOA condition, possibly reflecting a shift from configural to featural face processing. Together the results suggest that the human brain is highly specialized for processing emotional information and responds very rapidly to the brief presentation of expressive faces, even when these are located outside foveal vision.

Keywords: attention, cognitive control, emotion, eye movements, saccade programming

1.2 Introduction

Converging evidence suggests that emotional stimuli are preferentially processed (for reviews see Compton, 2003; Palermo and Rhodes, 2007; Vuilleumier, 2005) in that they both attract attention more rapidly (e.g., Lavie, Ro and Russell, 2003; Morand, Grosbras, Caldara and Harvey, 2010) and retain attention for longer (Bindeman, Burton and Jenkins, 2005; Georgiou, Bleakley, Hayward *et al*., 2005) than do non-emotional stimuli. Furthermore, the findings of a number of studies imply that the human brain is capable of processing emotional stimuli “pre-attentively” (see LeDoux, 1996; Morris, Öhman and Dolan, 1998; Öhman, 2002; Williams *et al*., 2006; and for a review see Tamietto and De Gelder, 2010).

The fact that the brain appears able to rapidly direct attention towards emotional stimuli raises interesting questions about the extent to which emotional stimuli that fall in peripheral (non-foveal) vision are processed, given the steep decline in visual acuity that occurs as stimuli are located more eccentrically. Several studies have sought to determine this by presenting such stimuli at different peripheral locations. For example, rapid eye movements towards a cue that could appear in one of two opposite hemifields (these types of eye movements are known as “prosaccades”- see Richards, 2003) are faster to positive emotional scenes than to neutral scenes presented 4.1˚ to the left or right of a central fixation cross (Kissler and Keil, 2008). In addition, De Cesarei, Codispoti and Schupp (2009) report that passively viewed emotional scenes presented as briefly as 24 ms, and positioned non-foveally up to 8.2˚ from fixation can elicit modulation of the electrical activity (event related potentials) generated by the brain during the experimental trials. Comparable modulation did not occur for neutral scenes presented at the same eccentricity, suggesting that the emotional content of a scene can be encoded (or that some discrimination between emotional and neutral scenes can occur) even when scenes are presented up to 8.2˚ from fixation.

It is generally agreed that a combination of both exogenous factors (such as a sudden change in luminance) and endogenous factors (such as expectations or memories of an object’s location) combine to influence the allocation of attention to specific scene regions (see Hutton, 2008 for a review). Given that the exogenous properties of the visual scene that feed into saccade programming are, by their very nature, being processed in non-foveal areas of the retina, a key question for researchers is what types of information can be extracted from peripheral vision and then used to guide saccades. Nummenmaa, Calvo and Hyöna (2009) directly investigated the extent to which extrafoveally presented emotional scenes influence saccade programming. An initial screen consisted of a central fixation cross with a rectangle either side. Participants fixated the central cross until they saw a cue (an abrupt luminance change to the outline of one of the rectangles). They were asked to look as quickly as possible to this cue (make a prosaccade). Either simultaneously with or 150 ms before the cue occurred, images of natural scenes appeared inside both rectangles. One of the scenes was always emotional (positive or negative) and the other always neutral. Nummenmaa *et al*. (2009) found that prosaccades were faster to cued rectangles containing emotional (positive or negative) scenes (congruent trials) than neutral scenes (incongruent trials) even at 0 ms stimulus onset asynchrony (SOA). It was argued that the content of emotional information presented in peripheral vision can be encoded prior to saccade onset, and that this early acquisition of information from stimuli that have not yet been fixated can influence the latencies of prosaccadic eye movements towards a simultaneous exogenous cue.

The stimuli used by Nummenmaa *et al*. (2009) were complex emotional (positive or negative) and neutral scenes taken from the International Affective Picture System (IAPS) (Lang, Bradley and Cuthbert, 2005). Given that visual acuity diminishes rapidly with increasing eccentricity from the point of fixation, their finding begs the question as to exactly what information was extracted from the peripherally presented scenes that led to the facilitation of saccades. The "emotional" IAPS scenes used in the study vary greatly in terms of their content, and indeed the emotions they portray and elicit. Furthermore, complex emotional scenes used to evoke the same emotional response (e.g., fear) can vary greatly in their content. Two scenes that are equally fear-eliciting and "threatening" in nature, may be visually very distinct from each other, and it is not clear whether the decrease in prosaccade latencies in the congruent trials is the result of a rapid "gist" based representation of the entire scene or a more detailed perception of a specific feature within the scene (such as a weapon, for example) (see Wolfe, 1998). The Nummenmaa *et al.* (2009) study found no effect of emotional valence- saccades were faster to both positive and negative emotional images compared to neutral images, and it is unclear whether the saccadic facilitation they observed is moderated by specific emotions or by how threatening the scenes were.

Many studies that have explored how the brain processes emotional information have used emotional faces rather than emotional scenes as stimuli. There is considerable converging evidence that face information is processed in dedicated brain areas such as the fusiform face area (see e.g., Rhodes, Byatt, Michie and Puce, 2004). In addition, faces appear to attract attention particularly rapidly – for example, Crouzet, Kirchener and Thorpe (2010) found that participants could initiate saccades towards faces in less than 150 ms after image onset and Devue, Belopolsky and Theeuwes (2012) have shown that irrelevant faces can capture eye movements during a simple visual search task. Faces have a number of advantages over complex scenes - unlike the IAPS scenes, faces depicting specific emotions have characteristic visual properties. For example, fearful faces have widened eyes and angry faces have contracted eyebrows allowing for more control in matching the appearance of the stimuli used within and between different affect conditions. In addition, emotions such as anger, fear, happiness (Ekman, 1999) and more complex emotions such as anxiety (Perkins, Inchley-Mort, Pickering *et al.*, 2012) can be universally recognised from facial expression. In contrast, the same universal labelling of certain scenes as being associated with unique emotions does not exist- a scene may be considered disgusting by one person but not another. Finally, both emotional and neutral faces consist of the same basic constituent parts (e.g., two eyes, one nose, one mouth etc.), whereas emotional and neutral scenes can vary dramatically in constitution potentially resulting in significant difference in the content of scenes that fall within the same or different affect categories. In contrast, the variation in image properties between neutral and emotional faces is considerably more subtle than differences between neutral and emotional scenes. A tiny alteration to a person's mouth, for example, could completely change the emotion portrayed. It is currently unclear whether information about these very subtle changes to the configuration of facial features can be extracted from extrafoveal locations in the same way as the "gist" of complex scenes appears to be extracted from peripheral vision in the Nummenmaa *et al.* (2009) study.

Nummenmaa *et al*. (2009) found that complex emotional scenes positioned 2.5 degrees to the left or to the right of a central fixation cross speeded up prosaccades to co-located targets when the scenes and saccade cue were presented simultaneously. In the current set of experiments we present task-irrelevant faces much further (6 degrees in experiment 1, and 4 or 12 degrees in experiments 2 and 3) from foveal vision. In order to determine whether specific emotions (as opposed to less specific differences between positive and negative valence) differ in their ability to influence prosaccade latency, we compared the effect of happy, angry and fearful versus neutral faces in our first experiment. It was predicted that saccade latencies to cues containing emotional faces would be faster than prosaccades to cues containing neutral faces. Saccade latencies were expected to be shorter in the -150 ms condition compared to in the 0 ms condition irrespective of whether an emotional or a neutral face is cued because the appearance of the faces serves as a warning for the onset of the cue in the -150 ms condition (see e.g., Ross & Ross, 1981).

1.3 Experiment 1

1.3.1 Method

Participants. 37 healthy participants (22 female; mean age 24 years) took part in the experiment. All participants were students at Sussex University and received either course credit or payment for their participation. All participants had normal or corrected-to-normal visual acuity. The study was approved by the University of Sussex Psychology and Life Sciences Research Ethics Committee.

Apparatus. Stimuli were presented on a 21-inch Sony CRT monitor with the refresh rate set to 60 Hz. Participants' eye movements were recorded using an EyeLink II lightweight, head-mounted eye tracker (SR Research, Ontario). The EyeLink II was set to monitor eye position at a rate of 500 Hz and has an average accuracy of 0.5˚. Eye event detection is based on an internal heuristic saccade detector built in the EyeLink tracker program. To detect a saccade, for each data sample, the built-in event parser computes instantaneous velocity and acceleration and a saccade is detected when these values exceed 30 degrees per second or 8500 degrees per second squared for two or more samples. A blink is defined as a period of saccade-detector activity with the pupil data missing for three or more samples in a sequence. Trials in which a blink obscured the primary saccade following target onset were excluded from analysis.

Materials. The face stimuli were sixteen greyscale photographs (transformed into JPEGs) selected from the Ekman and Friesen Pictures of Facial Affect (Ekman and Friesen, 1976). Each model appeared in four different photographs, one per facial expression considered (happy, angry, fearful and neutral). To ensure that low-level image characteristics would not confound the results, image statistics were obtained using MATLAB 7.0 (Math Works, Natick, MA) for the selected Ekman faces and the low-level visual properties of each were compared. One-way ANOVAs were run for each low-level image characteristic (contrast, luminance, energy, and root-mean-square) to assess whether any image property varied systematically with facial expression. None of the image characteristics varied by emotion (all Fs $\leq .882$, all p values $> .10$).

Stimulus displays. The initial display screen consisted of a horizontally and vertically centred white circular (unfilled) fixation target (1.5˚ in diameter) along with two vertically centred white (unfilled) rectangles, one positioned 2.5˚ to the right and the other 2.5˚ to the left of the central fixation point (measurement taken from centre of the fixation circle to the inner edge of the rectangle). These landscape oriented rectangles formed the saccade target areas and subtended visual angles of 10.54˚ x 7.98˚. The background colour was black. The imperative signal to the cued saccade target area was a change to the colour of the border of one of the rectangles from white to orange. The Ekman faces (oval cropped to remove non-facial information and placed on a black background) that appeared inside the saccade targets subtended 10.24˚ x 7.68˚. These distracter images filled the saccade target area but did not obscure the outline of the rectangle. Face pairs always consisted of one male and one female actor, and of one neutral face alongside either a fearful, happy or angry face.

Design. The experiment had a within subjects 2 (SOA: -150 ms or 0 ms) X 2 (Congruence: congruent when the cued rectangle contained an emotional face or incongruent when the cued rectangle contained a neutral face) X 3 (Emotion: happy, angry, fearful) design. The key dependent variable was time (in ms) taken to initiate a saccade to the cued target.

Procedure. After providing their informed consent to participate, the participants were seated approximately 60 cm from the monitor, the head-mounted eye tracker was fitted, and a brief calibration procedure was performed to ensure that the eye-tracker was accurate to at least the nearest 0.5˚. Before the experiment began, an instruction screen was presented to participants that explained that their task was to focus on the central fixation point at the start of every trial until the border of one of the two rectangles changed from white to orange at which point they should look as quickly as possible to the centre of the cued rectangle. Participants were also informed that some pictures would appear inside the rectangular frames, but that these had nothing to do with their task. Participants completed 12 practice trials before moving on to the experimental trials.

All trials began after a brief drift correction procedure. At this point a random delay between 0 and 100 ms (to reduce anticipations) was implemented. Then, in the 0 ms SOA trials the two face images appeared inside the two rectangular borders and simultaneously one of the rectangle borders turned orange. On trials with -150 ms SOAs, after the initial random delay the face picture appeared inside the rectangles and then 150 ms (9 retraces) later one of the rectangle borders turned orange. All trials timed out 1350 ms (81 retraces) after the onset of the imperative signal. At this point the initial display screen consisting of the fixation circle and the two rectangle frames (one either side) reappeared and the proceeding trial commenced again with the drift correct procedure. See figure 1 below.

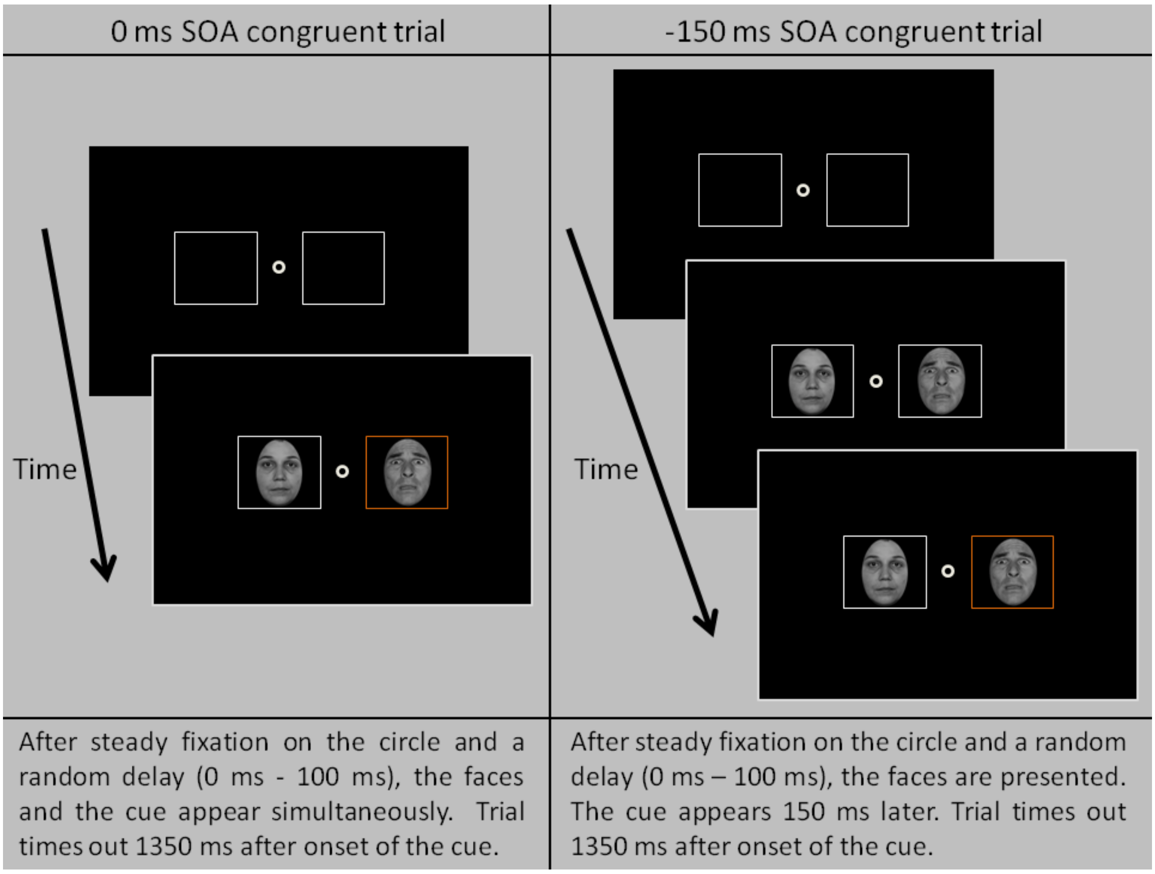

Figure 1: Sequence of events over time for a congruent trial with either a 0 ms or a -150 ms SOA

There were 192 experimental trials- 64 trials for each of the emotions (angry, fearful and happy) which were always paired with a neutral face. Half of the trials had a 0 ms SOA and half had a -150 ms SOA. The visual field to which the emotional and neutral face pictures were presented was counterbalanced across trials. Additionally, the visual field to which the male and female models in each picture pair were presented to was also counterbalanced across trials, as was cue side. Trials were presented to participants in random order and split into three blocks of 64 trials each. At the end of blocks one and two, the eye tracker was recalibrated.

Before leaving, all participants were fully debriefed about the hypotheses under investigation.

1.3.2 Results and discussion

Hierarchical linear modelling. In traditional statistical analyses the performance indices of interest (e.g., reaction times) are obtained by aggregating scores across trials of a given type for each participant. The means obtained from such aggregation are given equal weight in subsequent analyses despite the fact that the number of trials these means are based upon could vary greatly between participants and consequently loss of potentially interesting trial level information can occur. Traditional statistical approaches therefore are not ideal when data are multilevel, as they are here, with trials (level 1) nested within participants (level 2). Multilevel modelling approaches (Byrk and Raudenbush, 1992; Goldstein, 1995; Hox, 2002) allow each trial to be treated as an individual data point (avoiding aggregation) nested within a participant.

The basic multilevel model (adapted from Hox, 2002):

$$y_{ij} = \beta_{0j} + \beta_{1j}X_{ij} + e_{ij}$$

where β_{0j} is the usual regression intercept, β_{1j} is the regression coefficient for the explanatory variable X and e_{ij} is the residual error term. The subscript j is for level 2, the person level ($j = 1 \ldots J$) and the subscript i is for level 1, the trial level ($i=1 \ldots nj$). It is assumed that each person has a different intercept coefficient and a different slope coefficient (the j subscripts attached to the coefficients) and as such they are referred to as random coefficients (in standard analyses these coefficients are assumed not to vary). The explanatory trial-level variables are assumed here to be constant across participants (level 2 units). The residual error e_{ij} is generally assumed in multilevel models to have a mean of zero and an estimated variance.

All of the explanatory variables in the current analyses are at the trial level. It is possible in multilevel analyses to additionally consider explanatory variables at level 2 (here the person level), as well as interactions between level 1 and level 2 explanatory variables (cross-level interactions). For example, it would be possible to use multilevel modelling to consider individual differences in arousal (person level) and how this variable interacts with, for example, trial congruency (level 1), but this was not required for the purposes of the current experiments.

All multilevel analyses were carried out in the current experiments using HLM (version 6.04, SSI, Chicago). Significance tests were conducted using model deviance statistics that follow a chi-square distribution (with q degrees of freedom, where q is the difference in the number of parameters between the two nested models being compared). The variable of interest is always excluded from the reduced model.

Participants made faster prosaccades when the face appeared 150 ms compared to 0 ms before the target $\chi^2 = 1050.69$, $p < .0001$. Prosaccade latencies were faster when emotional faces appeared at the cued location compared to neutral faces $\chi^2 = 6.51$, $p < .05$. This effect was observed for both 0 and -150 SOAs. No other interactions or effects of emotion reached significance (all p values >.05). Prosaccade error rate was low (<5%) precluding any analysis of the effects of emotion or SOA on errors. Results are presented in figure 2 below.

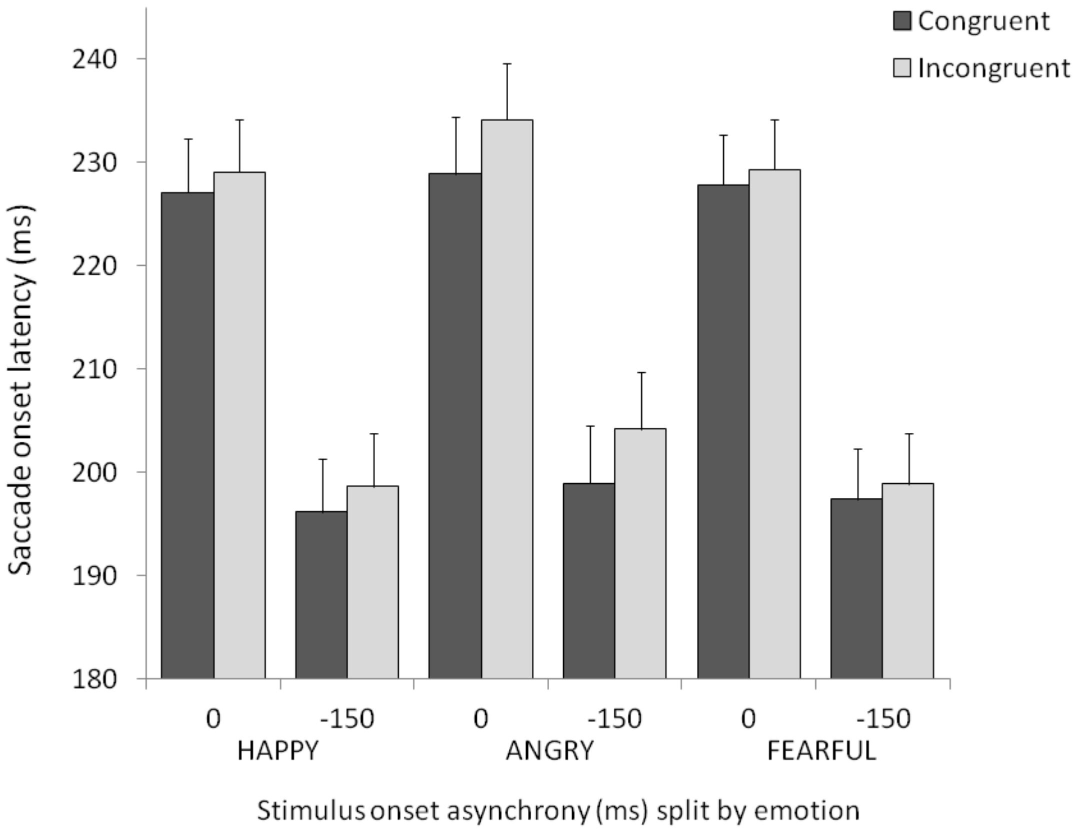

Figure 2: Mean saccade latencies for congruent and incongruent trials at both 0 ms and -150 ms SOAs split by emotion block (error bars represent SEs).

The results of experiment 1 replicate the Nummenmaa *et al*. (2009) finding that emotional information can be resolved sufficiently rapidly to speed prosaccades to target areas that contain emotional as compared to neutral information. Here we show that this effect extends to face stimuli in which the differences between the neutral and emotional stimuli are far more subtle than differences between scenes of contrasting valence. Consistent with Nummenmaa *et al*.'s results there was no systematic effect of emotion type on prosaccades, which raises interesting questions about what information is being resolved to speed prosaccades only to expressive faces, but not to neutral faces.

Given decreasing acuity with distance from the fovea, the aim of experiment 2 was to ascertain whether the congruency effect found in experiment 1 persists even when the face stimuli are presented at greater distal eccentricities. Since there was no effect of specific emotions on prosaccade latencies in experiment 1, we only used fearful faces as the "emotional" stimuli in experiment 2. This decision was guided by reports of a facilitative effect of fear on early visual processing (e.g., Phelps, Ling and Carrasco, 2006) as well as by the fact that presenting only the eyes of fearful faces for as little as 17 ms activates a greater response in the amygdala compared to when eyes from happy faces are presented. It was predicted that emotional faces presented closer to foveal vision would impact more on prosaccade performance than would the same stimuli presented further from fixation due to diminishing acuity at greater eccentricities from fixation.

1.4 Experiment 2

The apparatus used in experiment 2 was identical to those used in experiment 1. However, in order to assess whether the eccentricity of the target location affects prosaccades, some changes were made to the stimulus displays that were used in experiment 1. These are described below and illustrated in figure 3.

1.4.1 Method

Participants. 44 healthy participants (26 female; mean age 25 years) took part in experiment 2. All participants were students at Sussex University, had not taken part in experiment 1, and received either course credit or payment for their participation. All participants had normal or corrected-to-normal visual acuity. The study was approved by the University of Sussex Psychology and Life Sciences Research Ethics Committee.

Apparatus. Identical to experiment 1.

Stimulus displays. In the near condition the inner edge of the rectangular frames were positioned 4˚ from the central fixation point. In the far condition the distance between the central fixation target and the inner edge of the rectangle was 12˚. In order to allow for this degree of eccentricity from the central target in the far condition, the rectangles in experiment 2 were resized to subtend visual angles of 7.14˚ x 7.95˚. The emotional images used (pairs of Ekman faces) and their size (6.84˚ x 7.65˚.) remained the same as in experiment 1, see figure 3 below.

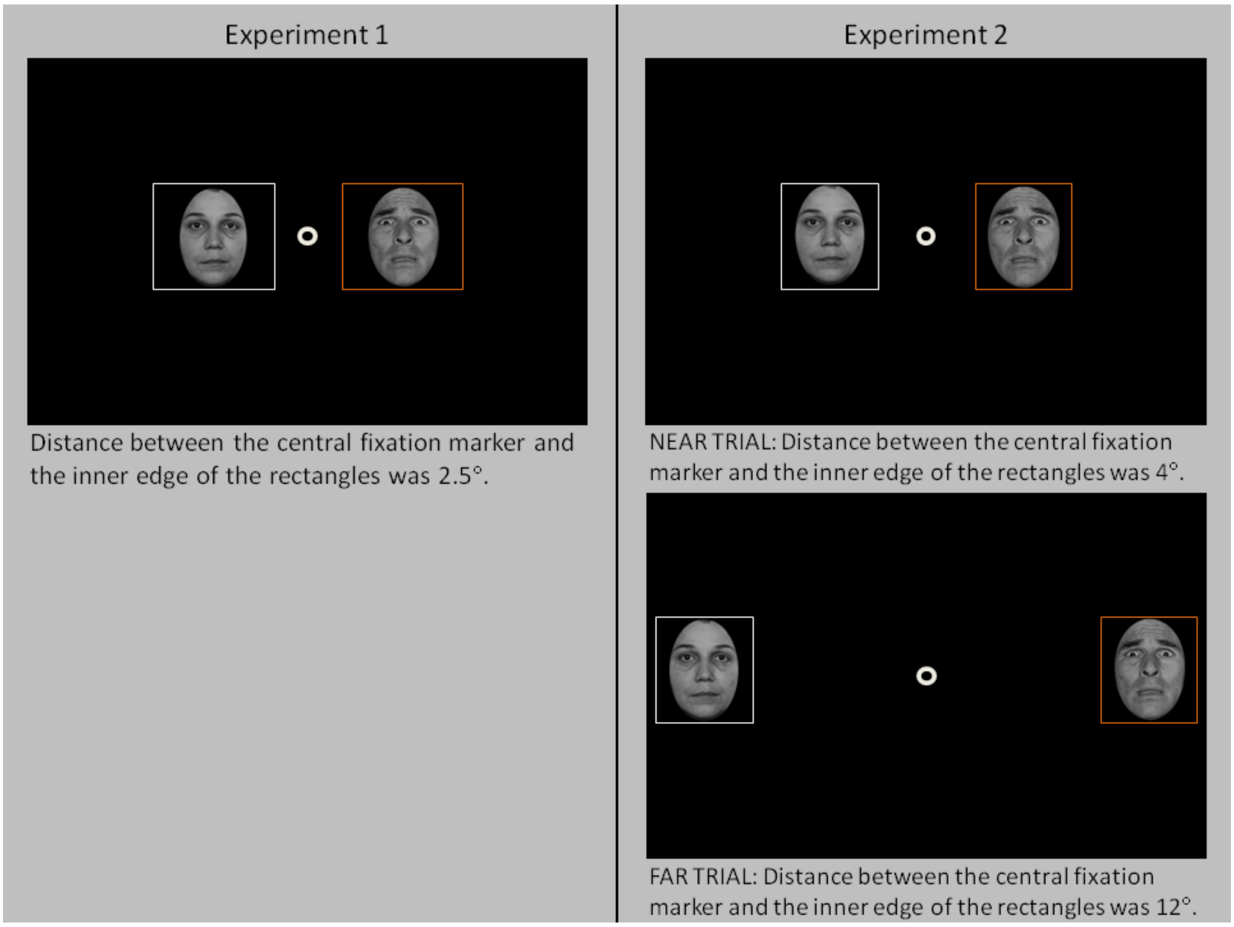

Figure 3: Stimulus displays in experiment 1 (left) and in experiment 2 near (right, upper) and far (right, lower) conditions.

Design. The experiment had a within subjects 2 (SOA: -150 ms or 0 ms) X 2 (Congruence: congruent when cued rectangle contained an emotional face or incongruent when the cued rectangle contained a neutral face) X 2 (Target location: near or far from centre fixation target) design. Near and far trials were intermixed.

The dependent variable was the time taken to initiate a saccade to the cued rectangle.

Procedure. The procedure was the same as in experiment 1 except for the following differences. The experiment had 192 experimental trials each consisting of a fearful face in one saccade target area and a neutral face in the other. On half of the trials both of the saccade target areas were close to the central fixation point and on half of the trials the two saccade targets were far (towards the outer edges of the screen) from the central fixation point.

1.4.2 Results and discussion

As in experiment 1, the effects of congruence and SOA were significant. Participants were faster to prosaccade towards the cue in the -150 ms SOA trials than in the 0 ms SOA trials $\chi^2 = 1307.56$, $p < .05$ and participants made faster saccades towards the cue in congruent compared to incongruent trials $\chi^2 = 12.83$, $p < .05$. Finally, saccades were faster in the near trials compared to the far trials $\chi^2 = 6.45$, $p < .05$. There was no eccentricity x congruence interaction. All other interactions were non-significant (all *p* values > .05). Results of experiment 2 are presented in figure 4 below. Prosaccade error rate was 4%.

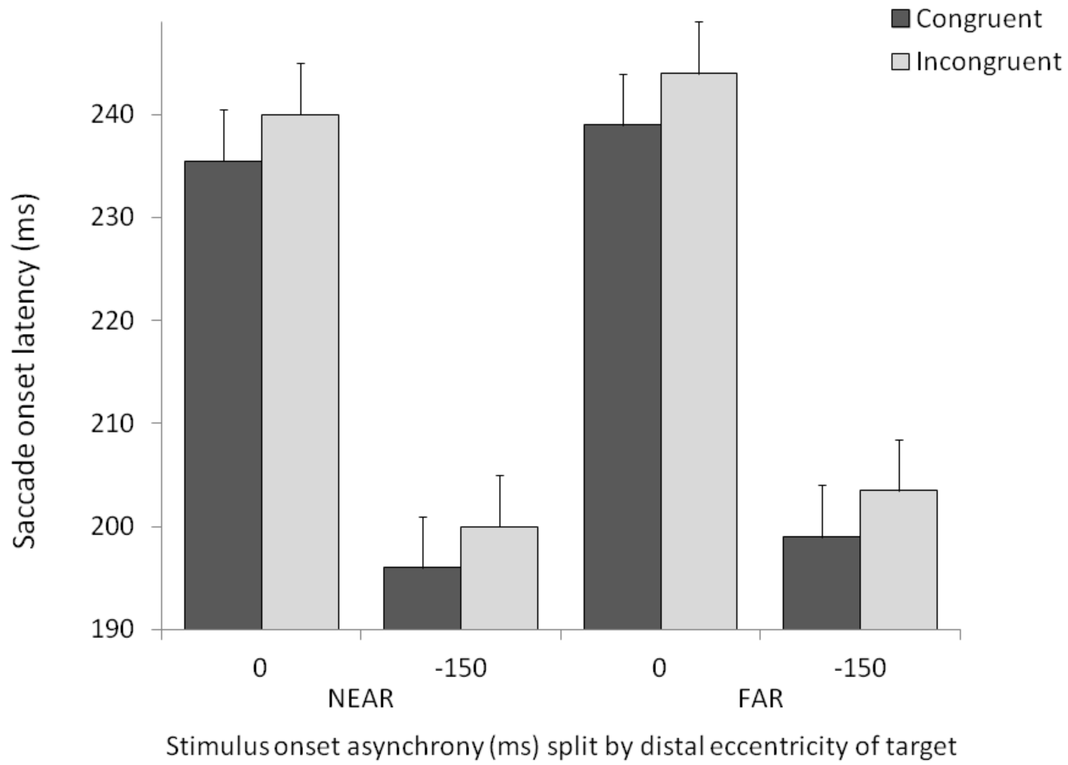

Figure 4: Mean saccade latencies for congruent and incongruent trials at both 0 ms and -150 ms SOAs split by near and far trials (error bars represent SEs).

The results of experiment 2 reveal a facilitative effect of fearful faces on prosaccades even when the face stimuli were presented up to 12 degrees from foveal vision, raising further interesting questions about exactly what information is extracted from parafoveally presented faces to elicit the reduction in prosaccade latencies. For example, are the faces processed holistically and semantic content (e.g., the emotion being expressed) extracted, or is the saccade facilitation driven by differences in low level visual properties of individual features of the face (such as a greater amount of white visible in the eyes of frightened faces)? Nummenmaa *et al*. (2009) postulate that the results of their 4th experiment (no decrease in saccade latencies to inverted emotional as compared to inverted neutral scenes), suggest that their findings cannot be explained by low-level visual properties. Indeed, there is evidence that inverting scenes disrupts scene processing (see e.g., Evans and Treisman, 2005). Similarly, inverting faces has been shown to disrupt configural processing and reliably interferes with the rapid encoding of facial affect (see Maurer, Le Grand and Mondloch, 2002 for a review). In our final experiment we sought to determine whether fearful faces still facilitate prosaccades when they are inverted. Given that the processing of inverted faces relies predominantly on featural processing which is typically slower than configural processing (see Hole and Bourne, 2010) it was predicted that an effect of congruency might emerge but only in the -150 ms trials in which more time is available to resolve the faces.

1.5 Experiment 3

1.5.1 Method

Participants. 28 healthy participants (all students at the University of Sussex, aged 18-40 years) who had not completed experiments 1 or 2 took part. Participants received either course credit or payment for their participation. All participants had normal or corrected-to-normal visual acuity. The study was approved by the University of Sussex Psychology and Life Sciences Research Ethics Committee.

Apparatus. Identical to experiments 1 and 2.

Stimulus displays. Stimulus displays were consistent with experiment 2 except that the emotional images (pairs of Ekman faces, subtending 6.84˚ x 7.65˚) were inverted (rotated by 180˚).

Design. The experiment had a within subjects 2 (SOA: -150 ms or 0 ms) X 2 (Congruence: congruent when cued rectangle contained an inverted emotional face or incongruent when the cued rectangle contained an inverted neutral face) X 2 (Target location: near or far from the centre fixation target) design.

The dependent variable was the time taken to initiate a saccade to the cued rectangle.

Procedure. The procedure was the same as in experiment 2.

1.5.2 Results and discussion

As in experiment 2, participants were faster to make prosaccades to the target in the near as compared to the far trials $\chi^2 = 20.04$, $p < .0001$. Consistent with the two previous experiments, participants were faster to correctly prosaccade on the -150 ms compared to the 0 ms trials, $\chi^2 = 253.85$, $p < .0001$. No main effect of congruency emerged despite the latencies being on average 3.6 ms faster in the congruent compared to the incongruent trials. However, the SOA x congruency interaction was significant $\chi^2 = 8.59$, $p < .01$ (see figure 5 below). In the -150 ms SOA condition but not in the 0 ms SOA condition, participants were faster to prosaccade on congruent trials. It appears then that participants needed longer exposure to the inverted faces prior to saccade initiation for a congruency effect to emerge. This may reflect a shift from configural processing to the slower feature-based processing of the face stimuli when they are inverted. No other interactions reached significance (all *p* values >.05). Prosaccade error rate was 3%.

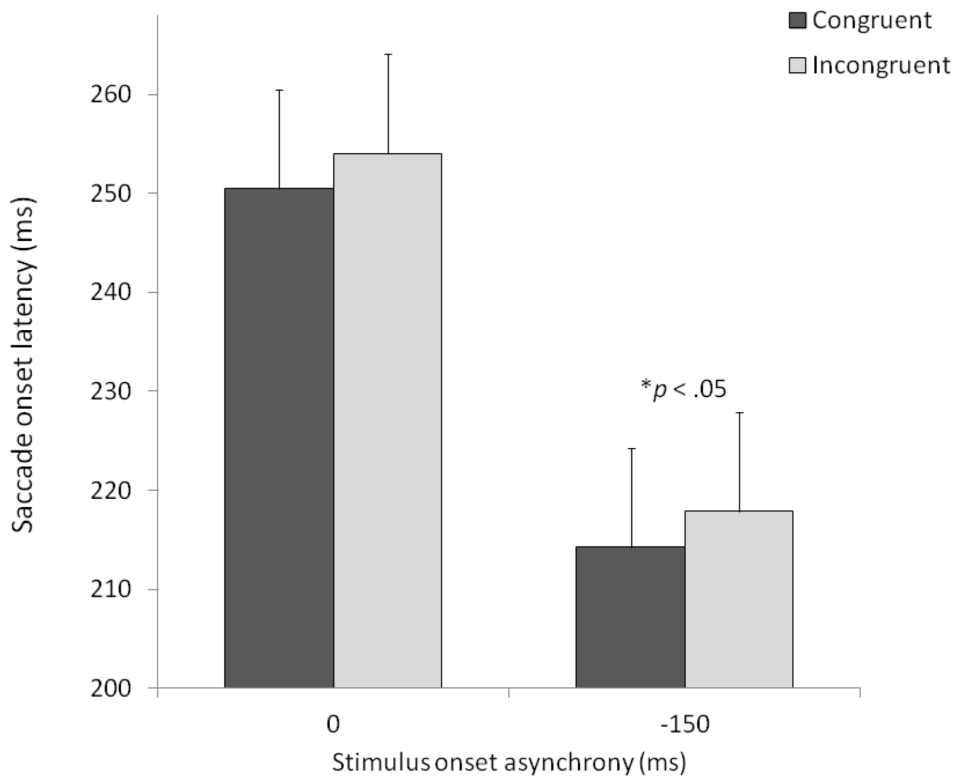

Figure 5: Saccade onset latencies as a function of SOA and congruency in experiment 3 in which inverted faces were used as stimuli (error bars represent SEs).

1.6 General discussion

We set out to explore whether parafoveally presented emotional faces could influence the early programming and execution of saccadic eye movements. Across three experiments we found that prosaccades initiated by cues that were co-located with an emotional face were faster than prosaccades initiated by cues co-located with a neutral face. In experiments 1 and 2, this facilitative effect of emotion on saccade latency occurred both when the faces appeared 150 ms before and simultaneously with the cue. In Experiment 3, in which the faces were inverted, this congruency effect only occurred in the -150 ms SOA condition.

The congruency effect observed at both SOAs in experiments 1 and 2 extends the findings of Nummenmaa *et al*. (2009) who showed that saccades towards complex emotional scenes were faster than those towards neutral scenes, even when the scenes and saccade cue were presented simultaneously. The authors interpreted this effect as evidence that high-level semantic information from emotional stimuli can be encoded even when it is perceived outside of foveal vision. However, the stimuli used by Nummenmaa *et al*. (2009) depicted complex scenes which varied considerably in content even within emotion categories. While in some scenes the emotional content was evident from facial affect, in others facial affect was partially occluded or non-existent. As a result, it is difficult to ascertain exactly what high-level semantic information led to the congruency effect, and more specifically, the extent to which it was dependent on rapid neural mechanisms involved in processing faces and facial affect. The experiments reported here used simple face stimuli, and despite the fact that the visual differences across facial emotions are far more subtle than the differences between complex scenes of contrasting valence, we were still able to observe a facilitative effect on saccade latencies to emotional compared to neutral stimuli. Our results are therefore consistent with other research demonstrating very rapid processing of facial affect, such as functional neuroimaging studies demonstrating heightened amygdala activity during very brief (17 ms SOA) exposure to emotional (happy and angry) as compared to neutral faces (Maxwell and Davidson, 2004).

On average it took participants in the current experiments around 200 ms to initiate prosaccades to the abrupt luminance changes in the -150 ms SOA trials and around 235 ms in the 0 ms SOA trials. The advantage for -150 ms SOA trials is consistent with a large number of studies demonstrating cueing or warning effects in prosaccades (see e.g., Fecteau and Munoz, 2007; Hutton, 2008 for a review) and a cueing effect of similar magnitude was also observed by Nummenmaa *et al*. (2009). Interestingly though, the average latency of prosaccades in the Nummenmaa experiments was somewhat slower than was observed in the present experiments, ranging from 240-250 ms in the -150 SOA condition and 260-270 ms in the 0 ms SOA condition. The faster average latencies observed in the present study may reflect the relative simplicity of our stimuli (faces compared to complex scenes) and again suggests the operation of comparatively rapid neural mechanisms that process facial affect.

It takes approximately 40 ms for visual information to be transmitted from the retina to the superior colliculus and approximately 20 ms for activation in the superior colliculus to trigger a saccade towards the cue, but average saccade latencies to simple targets are around 200 ms (see Carpenter, 1981). It is generally assumed that the “extra” time consists of on-going stimulus processing, facilitated by shifts in visual attention. The relationship between saccadic eye movements and visual attention is complex (see Hutton, 2008), but there is a general agreement that saccades to a selected target are preceded by a covert (without moving the eyes) attention shift to its location (see e.g., Rizzolatti, Riggio and Sheliga, 1994; Schneider, 1995). These covert shifts of attention were not restricted in the current experiment and, as Nummenmaa *et al*. (2009) argue, are likely to underlie the reduction in latency of saccades towards emotional content. The overall faster reaction times in congruent trials across experiments 1, 2 and partially in 3 may result from faster allocation of attention to cues containing the emotional face, or reaction times may be slower on incongruent trials because of the time it takes to disengage attention from the emotional face (see e.g., Moriya and Tanno, 2011; Georgiou, Bleakley, Hayward *et al*., 2005) that is positioned on the opposite side of the screen to the cue. It is also possible that a combination of both of these factors influence saccade latencies.

Given how little time was available to process the stimuli presented at the cue location in the 0 ms SOA trials, and the low visual acuity of parafoveally presented stimuli, interesting questions arise about exactly which aspects of the emotional faces were responsible for drawing attention towards them and the resulting facilitation of saccade latency towards the co-located cue. For example, were saccade latencies affected by a crude representation of the entire face based on some type of configural (first order, holistic or second order- see Maurer, Le Grand and Mondloch, 2002 for discussion) processing or by a featural analysis of the face, extracting information from isolated face regions (e.g. the eyes) that we have learned are most informative in evaluating facial affect? In Experiment 1 for example, happy, angry and fearful faces elicited a speeding effect on prosaccades and it is likely that this was driven by the extraction of information from learned informative face regions such as the mouth and eye regions to distinguish, even at a subliminal level, emotional from non-emotional faces. In support, Whalen *et al*. (2004) used fMRI to determine whether amygdala activity was related to the amount of white sclera visible around the pupil. Just the eyes were taken from images of fearful and happy faces and presented subliminally (17 ms, backward masked). Amygdala activity was significantly higher when eyes from fearful faces (with more visible sclera) were presented as compared to when eyes from happy faces (with less visible sclera) were presented. In addition, there is also evidence that the mouth region is most informative for detecting happy faces (e.g., Calvo and Nummenmaa, 2008).

In experiment 2, only fearful and neutral faces were used and the stimuli in the far trials were presented 12˚ eccentrically, thus relying more heavily on parafoveal regions of the retina than in experiment 1. These results suggest that low frequency information related specifically to the eye region of fearful faces may have driven the congruency effect in experiment 2. Recent research has found that the amygdala responds to the presentation of threat related stimuli presented outside of the focus of attention, and importantly, it is activated by low spatial frequency information (Vuilleumier, Armony, Driver and Dolan, 2003). Given the increased distal eccentricity of the faces in experiment 2, the observed facilitative effect of fearful faces would have required the decoding of very low acuity information extracted from parafoveal retinal regions which rely specifically on low frequency visual information. So one possibility is that the decrease in prosaccade latency we saw in experiment 2 was the result of rapid processing of low spatial information gleaned from the fearful face stimuli (most likely from the high contrast eye regions). This information likely activated a highly evolved neural and behavioural module for facilitating rapid responses to impending danger which, in this case, resulted in faster allocation of overt attention to the threat-related information (fearful face). When the neutral faces were cued, however, the same highly evolved threat-sensitive system was presumably not activated and as a result the allocation of overt attention to the cued neutral face was comparatively less rapid.

Our finding in experiment 3 that inverted emotional faces were still able to facilitate saccade processing stands somewhat in contrast to the results of experiment 4 of Nummenmaa *et al*. (2009), in which no differences in saccade latencies were found to inverted emotional scenes compared to inverted neutral scenes. Inverting faces interferes with configural but not with featural processing (Collinshaw and Hole, 2000; Yin, 1969). For example, after being familiarised with a series of faces participants were then more accurate at detecting whether a specific facial feature (e.g., a nose or mouth) belonged to one of the “familiar” faces when the facial feature in question was shown in the context of the whole face than when presented in isolation (Tanaka and Farah, 1993). The whole face advantage for recognising individual facial features implies that during the exposure period, the faces were processed holistically as opposed to featurally. Further, when the experiment was replicated with inverted faces, the whole face advantage for recognising individual facial features was no longer evident, suggesting that configural processing may be unique to upright faces. Several studies have shown that with more time facial emotion processing can still be achieved when faces are inverted based on a featural rather than a configural analysis (see Hole and Bourne, 2010 for discussion).

In experiment 3 an effect of congruency was found in the -150 ms SOA condition only. The lack of a congruency effect in the 0 ms trials suggests that the facilitation is not purely based on low-level stimulus properties, and its emergence in the -150 ms condition may reflect the extra processing involved in the change from configural to featural processing of the faces. The current set of experiments could be extended to investigate which features of the faces are necessary for the congruency effect to be observed. For example, by using only eyes (emotional versus neutral) as stimuli, or by directly manipulating the amount of contrast in key areas such as the eyes and mouth.

Taken together, the current findings support previous research suggesting that facial affect can be processed rapidly, and demonstrate that the processing is sufficiently rapid to influence the early stages of saccade programming. The results also suggest that the neural mechanisms involved in processing faces are sufficiently sensitive to be able to derive meaningful information concerning the emotional content even from the relatively low acuity information available when stimuli are presented in parafoveal vision.

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2. Misperceiving facial affect: Effects of laterality and individual differences in susceptibility to visual hallucinations.

2.1 Abstract

It has been suggested that certain types of auditory hallucinations may be the by-product of a perceptual system that has evolved to be oversensitive to threat related stimuli. People with schizophrenia and high schizotypes experience visual as well as auditory hallucinations, and have deficits in processing facial emotions. We sought to determine the relationship between visual hallucination proneness and the tendency to misattribute threat and non-threat related emotions to neutral faces. Participants completed a questionnaire assessing visual hallucination proneness (the Revised Visual Hallucination Scale – RVHS). High scoring individuals (N=64) were compared to low scoring individuals (N=72) on a novel emotion detection task. The high RVHS group were less accurate than the low RVHS group at discriminating emotional faces from neutral ones and were significantly more likely to identify neutral faces as being angry. There was a trend for all participants to misperceive neutral faces as being emotional when presented to the right visual field than to the left visual field. Our results support continuum models of visual hallucinatory experience in which tolerance for false positives is highest for potentially threatening emotional stimuli.

Keywords: emotion detection, emotion misattribution, face perception, hallucination proneness, hemispheric asymmetry, psychosis continuum, schizotypy

2.2 Introduction

Hallucinatory experiences are not confined to patients with schizophrenia, and recent research suggests they may be much more prevalent in the general population than previously thought, particularly among young adults (Rossler *et al*., 2007) and the elderly (Tien, 1991). Although auditory verbal hallucinations are most common in schizophrenia (e.g. Mueser *et al*., 1990), visual hallucinations still have a high lifetime prevalence in this disorder (Bracha, 1989), and are also observed in patients with other disorders such as Parkinson's disease (Barnes and David, 2001; Fenelon *et al*., 2000; Manford and Andermann, 1998). The prevalence of visual hallucinatory experiences in the general population is unclear, however, as most population studies either focus specifically on auditory hallucinations (e.g., Barkus, Stirling, Hopkins, Mckie and Lewis, 2007), or do not discriminate between auditory and visual hallucinations (e.g., Lincoln and Keller, 2008). One early exception is Sidgwick's "Census of Hallucinations", carried out on 17,000 "sane individuals" and published in 1894. Visual hallucinations were reported by approximately 6% of adults aged 20-29. In a more recent large-scale survey, 2.7% of 13,057 individuals reported experiencing visual hallucinations at least once in their life (Ohayon, 2000), but some individuals had a mental disorder present or an organic or toxic pathology involved, making the exact percentage of non-clinical participants difficult to ascertain. Together these surveys suggest that, like auditory hallucinations, visual hallucinations are also experienced by some non-psychotic individuals.

Healthy individuals who experience hallucination-like experiences are at higher risk for developing a schizophrenia spectrum disorder (see ; Delespaul and Krabbendam, 2009; Kelleher and Cannon, 2011; van Os, Linscott, Myin-Germeys *et al*., 2009, for reviews) providing support for the suggestion that a continuum exists between pathological hallucinatory symptoms and normal perceptual experiences (see e.g., Johns and van Os, 2001). Researchers have explored the cognitive processes underlying auditory hallucinatory experiences in healthy participants by measuring performance on tasks designed to elicit “false positive” responses. Such tasks typically involve detecting the presence of a target signal (such as a tone or a spoken word) embedded in some background noise. Bentall and Slade (1985) for example, found that people with schizophrenia and students with a higher disposition to hallucinating (based on a self-report questionnaire) made more false positives in an auditory signal detection task. The rationale behind this approach is that false positive responses and hallucinatory experiences both indicate that a participant believes they have seen or heard something that in reality was not present.

Just as the majority of questionnaire and interview studies of hallucinatory experiences in non-clinical populations focus on auditory rather than visual hallucinations, the majority of studies investigating false positive errors in healthy participants have used auditory rather than visual stimuli. One exception is Reed *et al*. (2008) who asked healthy participants to perform a word identification task in which word and non-word letter strings were presented briefly on screen. High schizotypes made significantly more false positive errors (claiming to have seen a word when a non-word was presented) than low schizotypes, but this effect of schizotypy score did not interact with stimulus ambiguity (fast vs. slow stimulus presentation). These results suggest that the tendency for high schizotypes to make increased false positive errors in signal detection type tasks may extend to the visual modality and can be observed even when visual stimuli are not highly perceptually ambiguous.

One area of visual perception in which patients with schizophrenia and high schizotypes have known deficits is facial affect recognition (e.g., Phillips and David, 1997; Williams, Loughland, Gordon and Davidson 1997; and see Edwards, Jackson and Pattison, 2002 and Phillips and Seidman, 2008 for reviews). In addition to impairments in accurately detecting facial emotions, there is also some evidence to suggest that individuals with schizophrenia and high schizotypes are more likely to make false positive errors (seeing emotions in neutral faces) than are healthy controls and low schizotypes respectively. Importantly, this tendency may be limited to “threat-related” emotions – anger, fear and disgust. For example, Kohler *et al*. (2003) found that individuals with schizophrenia were more likely to misattribute fear and disgust to neutral faces than were the controls, and Van Rijn *et al*. (2010) found that individuals at ultra-high risk of developing schizophrenia were more likely to label neutral faces as angry. Participants scoring highly on the disorganised schizotypy subscale are more likely to perceive neutral faces as expressing negative emotions (Brown and Cohen, 2010). Similarly, Van't Wout, Aleman, Kessels, Laroi and Kahn (2004) found that the likelihood of making erroneous classifications of non-threatening (happy) faces as threatening, when using degraded (reduced visual contrast) faces as stimuli, correlates positively with healthy individuals' scores on the Unusual Perceptual Experiences schizotypy subscale. Together these findings support the recent suggestion that certain types of hallucinatory experience may be the by-products of a cognitive system that has evolved to detect threats (Dodgson and Gordon, 2009). There have, however, been no studies that have set out to directly test this hypothesis in the visual domain, and to address the relationship between individual differences in proneness to visual hallucinatory experiences and the tendency to ascribe threat-related emotions to neutral faces.

A large body of evidence suggests there is a right hemisphere advantage for processing facial emotion, and indeed face processing in general (see Hole and Bourne, 2010). For example, Bourne (2008) used pairs of chimeric faces (in which one half of a vertically split face is neutral and the other emotional), and found that participants showed a bias towards choosing the face in which the emotion is expressed in the left visual field when asked which of the two faces is the more emotive. Whilst a right hemisphere advantage for detecting facial emotions appears well established, it is not clear whether similar lateralization effects influence the likelihood of misattributing emotion to neutral faces – in other words whether participants are more likely to see non-existent emotions in neutral faces presented to the left or right visual field.

In contrast to the left hemifield bias for face processing observed in healthy participants, patients with schizophrenia have been found to display a significantly reduced asymmetry or indeed no hemifield bias at all for facial emotions (Kucharska-Pietura, David, Dropko and Klimkowski, 2002). David and Cutting (1990) asked patients with schizophrenia to decide whether happy-sad chimeric faces depicted a happy expression or a sad one. Unlike the controls, who showed the expected left-hemifield bias, the schizophrenia group had no bias in either direction. The left-hemifield bias when viewing chimeric faces is similarly attenuated in those who have higher negative schizotypy (social anhedonia) scores (Luh and Gooding, 1999). However, the literature documenting decreased right hemisphere dominance in people with schizophrenia and in high schizotypes is not consistent. For example, Leonards and Mohr (2009) tracked participants' eye movements and found that elevated positive schizotypy (magical ideation) was associated with an increased bias in initial saccade landing positions towards the left side of the face.

In this study we developed a task in which pairs of faces were briefly presented in participants' left and right visual fields. On half of the trials one of the two faces displayed an emotion (happiness, anger or fear) and the other was neutral. On the remaining trials, both faces were neutral. Participants were asked to indicate whether or not an emotional face was present and if so which of the two faces was emotive. The task thus allowed us to measure participants' tendency to make false positive responses (ascribing emotions to neutral faces) as well as their accuracy (correctly identifying the location of an emotional face). We explored the effects of visual hemifield, facial emotion and individual differences in proneness to visual hallucinations on these two measures. All participants were expected to make more false positive responses to neutral faces appearing in the right visual field, and given the reduced left hemifield bias observed in patients with schizophrenia and high schizotypes in the majority of research described above, it was anticipated that high schizotypes would show a reduced left hemifield bias for emotion detection compared to low schizotypes. Finally, if as has been suggested, "hypervigilance hallucinations" reflect an oversensitivity to threat related information, then false positives should be higher in blocks of trials containing angry and fearful faces compared to happy faces, particularly for participants who are prone to visual hallucinatory experiences.

2.3 Method

2.3.1 Participants. 136 participants were selected from a pool of 259 healthy participants based on their answers to a subset of items from the Revised Hallucination Scale (Morrison *et al*., 2000). This 15 item scale contains 6 items scored on a 4 point scale that deal specifically with visual hallucinations. Scores on these 6 items were summed to create an index of proneness to visual hallucinatory experiences we have termed the “Revised Visual Hallucination Scale” or RVHS. The 136 selected participants were those whose scores fell in the lowest and highest quartiles of all 259 scores, forming a low RVHS group (Mean score = .96, SD = .91; N = 72; 55 female; mean age = 20.1 years, SD = 2.81, age-range = 18.2 - 35.3 years) and a high RVHS group (Mean score = 8.4, SD = 2.6; N=64; 57 female; mean age = 20.3 years, SD = 2.90, age-range = 18.3 - 39.17 years) respectively. All participants also completed two further inventories: those questions on the Revised Hallucination Scale related specifically to auditory hallucinations and the Brief Schizotypal Symptoms Inventory (SSI), (Hodgekins *et al*. 2012). All participants were students at Sussex University and had normal or corrected-to-normal vision. The University of Sussex ethics board approved the study.

2.3.2 Materials. Stimuli consisted of 16 greyscale images selected from the Ekman and Friesen Pictures of Facial Affect (Ekman and Friesen, 1976). The photographs were cropped so that no hair was visible, and then resized to fit on a dark grey background measuring 178 x 196 pixels. For each emotion (happy, angry, fearful and neutral), 2 male and 2 female faces were used. Faces were masked after presentation with a greyscale image consisting of 8 x 8 pixel squares randomly selected from the neutral faces, and then randomly combined to form a single image with the same dimensions as the face stimuli. Stimuli were presented using Experiment Builder software (SR Research, Ontario) on IBM compatible PCs with 17-inch TFT monitors.

To ensure that low-level image characteristics were equated across stimuli, image statistics were obtained using MATLAB 7.0 (Math Works, Natick, MA) for the selected Ekman faces and the low-level visual properties (skewness, luminance, contrast, root mean squared, kurtosis and energy) compared. One-way ANOVAs revealed that none of the image characteristics varied by emotion (all *F*s ≤ .882, all *p* values > .10).

2.3.3 Design*.* The experiment had a mixed design. The within subjects factors were: hemifield of presentation (left or right) and target emotion (happy, angry or fearful). RVHS scores (high vs. low) were a between subjects factor. The dependent variables were the number of false positive errors made on the neutral-neutral trials and overall number of correct responses on the target present trials. There were three experimental blocks, one for each target emotion. Participants were informed of the target emotion at the start of each block.

2.3.4 Procedure. Participants were seated approximately 60 cm from the monitor. All trials began with participants focussing on a central fixation cross. A random delay between 0 and 1250 ms (to reduce anticipations) followed. Then, the two face images appeared simultaneously onscreen one each side of the central cross and remained onscreen for 250 ms before being masked. There were 192 experimental trials, 64 trials in each block (angry, fearful and happy). Half of the trials in each block were neutral-neutral trials in which no emotional face was present. The remaining trials consisted of one emotional and one neutral face and half of the time the emotional face was presented to the left hemifield and half of the time the emotional face was presented to the right hemifield. The horizontal eccentricity of the faces was varied such that in each block half of the trials were near trials in which the centre of the face stimuli were 6.5 cm (6^{o}) to the right or left of the centre of the screen and half of the trials were far trials in which face stimuli were presented 13 cm (12^{o}) to the right or left of the screen centre. All face pairs consisted of one male and one female actor and the visual field to which the male and female models in each picture pair were presented was also counterbalanced across trials.

Participants were asked to press the ‘f’ key if they thought the face on the left was an emotional face, the ‘j’ key if they thought the face on the right was emotional, and the spacebar if they thought both faces appeared neutral in expression. There were three blocks of trials. The target emotion (angry, happy or fearful) varied across blocks and the order in which the blocks were completed by each participant was randomised. Participants completed 4 practice trials at the start of each block.

Participants also completed the Revised Visual Hallucination Scale (RVHS) which consists of the 6 items (listed below) from the Revised Hallucination Scale (Morrison *et al*., 2000) that deal specifically with visual hallucinatory experiences:

1. The people in my daydreams seem so true to life that I think they are real.
2. I have seen a person’s face in front of me when no one was there.
3. When I look at things they appear strange to me.
4. I see shadows and shapes when there is nothing there.
5. When I look at things they look unreal to me.
6. When I look at myself in the mirror I look different.

The Revised Auditory Hallucination Scale (RAHS) which consists of those items from the Morrison *et al*.’s (2000) Revised Hallucination Scale that deal specifically with auditory hallucinatory experiences, and the brief Schizotypal Symptoms Inventory (SSI) (Hodgekins, 2012), a general measure of schizotypy, were also completed.

2.4 Results

Signal detection theory was used to assess participants' sensitivity to the detection of emotional stimuli as well as their response bias (the tendency to give positive responses regardless of whether an emotional face was present or not).

The following signal detection measures were calculated:

Hit rate

How frequently a participant correctly identified the emotional face on trials with one emotional and one neutral face presented. Hit rate was calculated using the following equation:

$$\textit{Hit rate} = \frac{hits}{hits + misses}$$

False alarm rate

How frequently a participant responded positively on trials in which no emotional face was present. False alarm rate was calculated using the following equation:

$$\textit{False alarm rate} = \frac{false\ alarms}{false\ alarms + correct\ rejections}$$

Sensitivity (d')

In order to assess each participant's ability to discriminate an emotional face from a neutral face, d' (d prime) was calculated using the formula below. The smaller the d' the greater the participant's tendency to misperceive neutral faces as emotional. Larger d' values indicate higher sensitivity in distinguishing neutral faces from emotional ones.

$$d' = \phi^{-1}(H) - \phi^{-1}(F)$$

Where ϕ^{-1}(H) is the *z* score corresponding to the hit rate and ϕ^{-1}(F) is the z score corresponding to the false alarm rate.

Response bias (β)

Each participant's response bias was calculated using the following equation:

$$\beta = e\left(\frac{[\phi^{-1}(F)]^2 - [\phi^{-1}(H)]^2}{2}\right)$$

The lower the value of β is, the more likely it is that a "yes" response will be given (regardless of whether or not the target actually is present).

2.4.1 Accuracy: discriminating emotional faces from neutral faces.

A mixed design analysis of covariance (ANCOVA) was conducted on the sensitivity (d') data. The between subjects factor was RVHS group (high vs. low). To control for other schizotypal traits and auditory hallucination proneness that may covary with RVHS, SSI scores and scores on the items in the Revised L-S Hallucination Inventory relevant to auditory hallucinations were added to the model as covariates. Emotion (happy, angry, or fearful) and visual field (left vs. right) were the two within-subjects factors. Although eccentricity of the face stimuli was manipulated, data for the near and far trials were collapsed and in order to simplify interpretation, eccentricity was not entered as a factor into the ANCOVA.

The mean sensitivity (accuracy) scores for each emotion were as follows: Happy (Mean = 2.88, SE = .05), Angry (Mean = 2.12, SE = .06), Fearful (Mean = 1.93, SE = .05). There was a highly significant main effect of emotion $F(2,258) = 24.60$, $p < .01$ (see figure 1). Bonferroni corrected planned comparisons revealed that happy faces were detected more accurately than both angry faces *t*(260) = 18.38, *p* < .01 and fearful faces *t*(260) = 14.45, *p* < .01 and that angry faces were detected more accurately than fearful faces *t*(260) = 3.8, *p* < .01.

The mean accuracy score for faces presented to the left visual field was 2.44 (SE = .05) and to the right visual field was 2.18 (SD = .05).There was a main effect of visual field on accuracy such that individuals were more competent at discriminating neutral faces from emotional faces when faces were presented to the left visual compared to when presented to the right visual field *F*(1,129) = 7.44, *p* < .01.

There was also a significant emotion x laterality interaction *F*(2,258) = 3.08, *p* < .05 revealing that although the left visual field advantage for detecting emotional faces was evident in all emotion blocks, it was particularly pronounced in the threat-related angry *t*(260) = 4.37, *p* < .01 and fear t(260) = 6.186, *p* < .01 blocks compared to in the happy block *t*(260) = 1.78, *p* < .05.

The mean accuracy score for the high and low RVHS groups were 2.15 (SE = .08) and 2.47 (SE = .08) respectively. There was a main effect of RVHS group on sensitivity scores. The high RVHS group were significantly less competent at discriminating emotional faces from neutral ones than the low RVHS group *F*(1,129) = 5.865, *p* < .05. RVHS did not interact with any of the other variables. The two covariates were not significantly related to emotion detection.

There were no other statistically significant main effects or interactions.

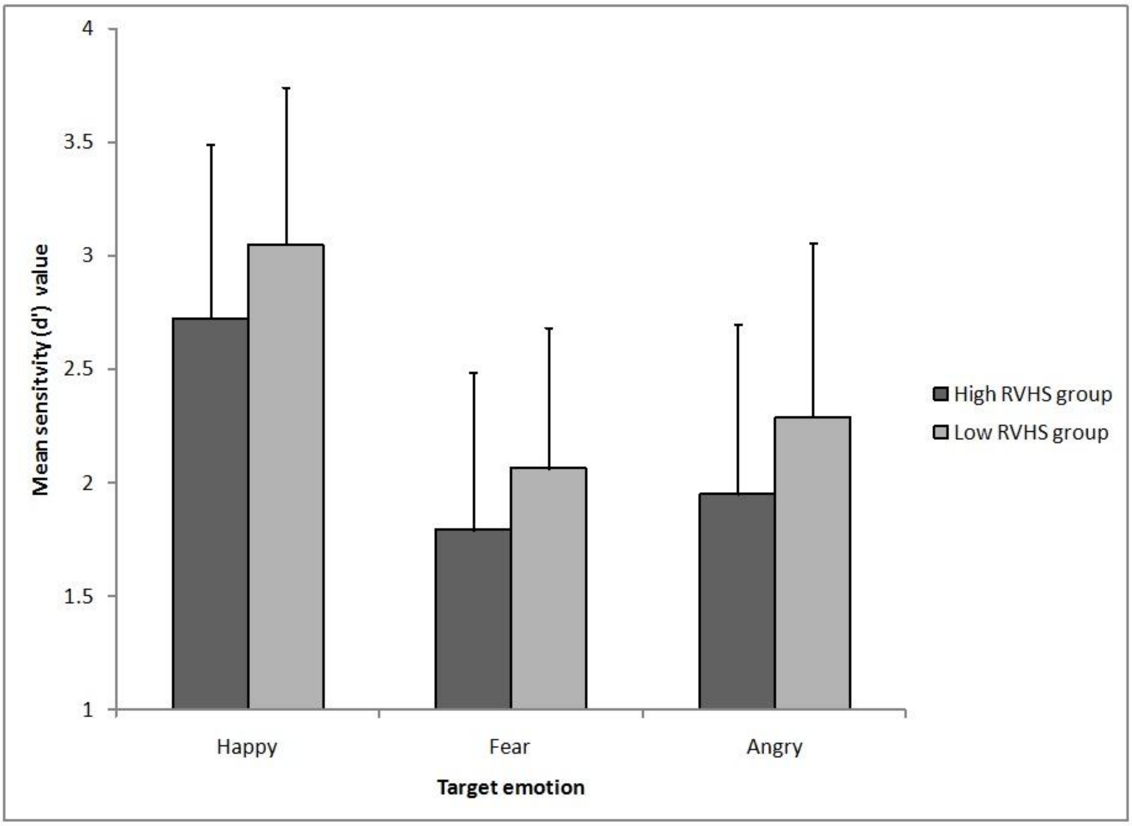

Figure 1. Mean d'prime sensitivity score as a function of emotion and RVHS group. Covariates appearing in the model are evaluated at the following values: SSI = 17.74, auditory hallucination proneness = 6.68. Error bars represent standard deviations.

2.4.2 Errors: decision-making (response) bias (β)

There were no significant main effects of emotion or RVHS score on response bias. The two covariates were not significantly related to response bias. There was a trend for participants to make more false positive errors to faces presented to the right than to the left visual field $F(1,129) = 2.99$, $p = .09$. Finally, there was a significant emotion x RVHS interaction $F(2,258) = 5.50$, $p < .05$. Multiple comparisons revealed that there were no significant differences in response bias between high and low RVHS in the happy or fear blocks, but in the angry block the high RVHS were more likely to make false positive errors, $t(260) = 2.58$, $p < .05$ (see figure 2). No other interactions in the response bias model were statistically significant.

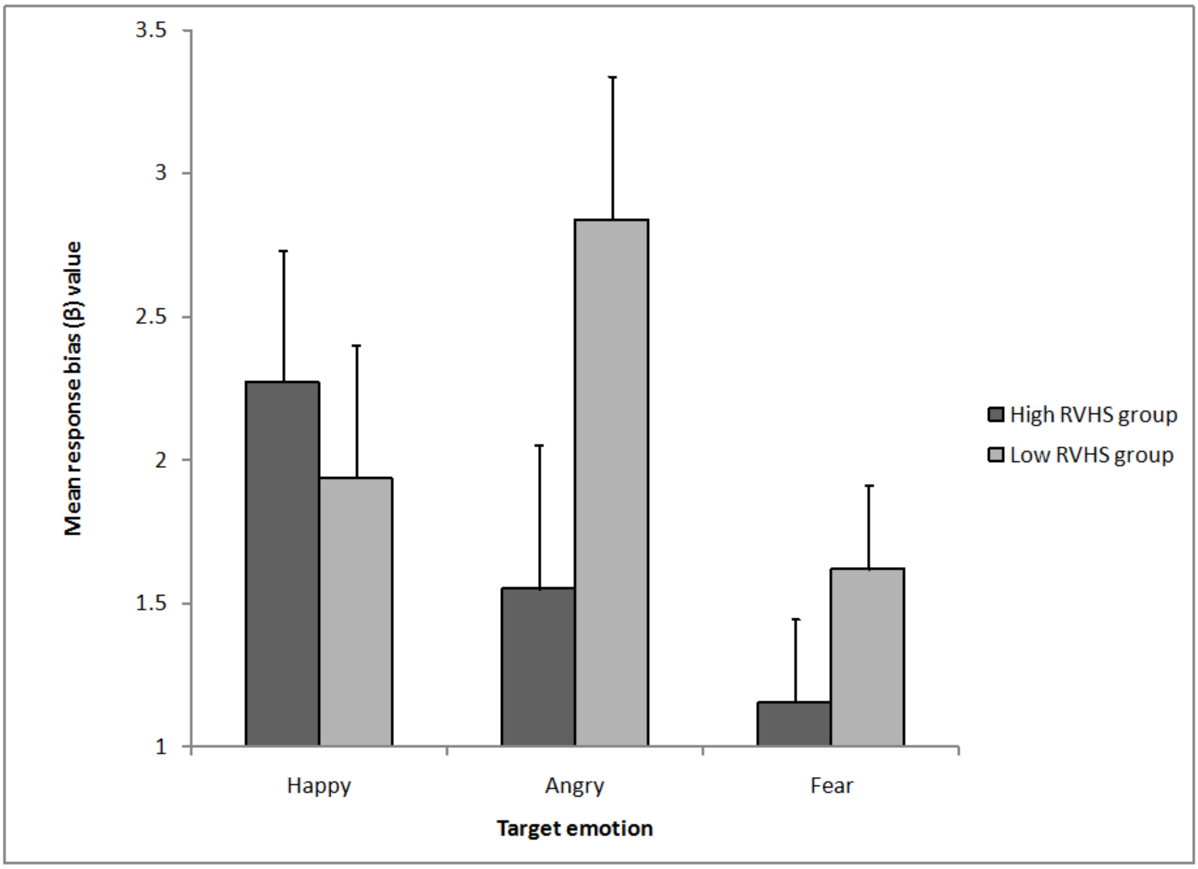

Figure 2.Mean response bias (β) as a function of emotion and RVHS group. Covariates appearing in the model are evaluated at the following values: SSI = 17.74, auditory hallucination proneness = 6.68. Error bars represent standard deviations.

2.5 Discussion

Using a novel experimental task, we set out to determine the relationship between facial emotion processing, laterality and individual differences in susceptibility to visual hallucinations. Several key findings emerged. Our task was successful in generating false positive responses to neutral faces in all experimental blocks - participants mistook neutral faces as being happy, angry and fearful. Importantly, those participants with high scores on the RVHS were significantly more likely than low scoring participants to misperceive neutral faces as angry. There was a trend for more misperceptions to occur when neutral faces were presented to the right visual field than to the left visual field. The task also allowed us to look at emotion detection accuracy. Correct detection of emotional faces was higher in the happy block than in the angry and fear blocks. The high RHVS group were less accurate than the low RVHS group at discriminating expressive faces from neutral ones regardless of the emotion being expressed. All participants were more accurate at detecting emotional faces presented on the left than on the right, and this left visual field advantage was particularly pronounced for the threat-related faces.

The finding that healthy participants who are more visual hallucination prone are more likely to misperceive neutral faces as being angry extends previous research which has found that the erroneous classification of non-threatening faces as threatening is inflated in people with schizophrenia (Kohler *et al*., 2003), ultra-high risk adolescents (van Rijn *et al*., 2010) and high schizotypes (Brown and Cohen, 2010; Van't Wout *et al*., 2004). These findings support suggestions that our perceptual system has evolved to tolerate misperceptions (false positives) when an individual perceives imminent threat (Dodgson and Gordon, 2009). According to this argument, tolerance of false positives to threat but not non-threat stimuli has evolved because the possible negative consequences of failing to detect a threat stimulus in the environment are much worse than failing to detect non-threatening stimuli. The result is a susceptibility to what Dodgson and Gordon term "hypervigilance hallucinations". The fact that the content of pathological hallucinations is frequently described as hostile and threatening in nature by people with schizophrenia (Nayani and David, 1996) provides some support for this contention.

We did not observe higher false positive rates in the fear block suggesting that any hypervigilance to threat observed in the current experiment is specific to a direct threat from another (angry) individual rather than some less specific type of impending threat in the environment (as indicated by a fearful face). In the present study, we provide further support for the hypervigilance hypothesis by showing that the tendency to falsely see anger on neutral faces is most apparent in individuals who report comparatively high levels of visual hallucinatory experiences. In addition, patients with schizophrenia frequently report visual perceptual anomalies such as flooding or sensory overload (see Bunney *et al*., 1999; McGhie and Chapman, 1961) and differences between the high and low RVHS groups in their ability to gate or filter the emotional stimuli presented, particularly in the angry block, may be a contributing factor here. Future research into the relative roles of low-level perceptual anomalies and higher-level cognitive biases on misperceptions of threat is therefore encouraged.

Consistent with previous research (e.g., Phillips and David, 1997; Williams *et al*., 1997) the high RHVS group were less accurate at discriminating emotional faces from neutral ones. Whilst the ability to correctly identify an emotion when it is present and the tendency to misperceive an emotion when it is absent might be expected to correlate, our data suggest that they are, at least to some extent, independent processes since the high RVHS group only showed inflated false positive rates in the angry block but were less accurate at discriminating emotional faces from neutral ones in all three emotion blocks.

All participants were most accurate at detecting happy faces, a result that replicates a large amount of research suggesting happiness is the easiest emotion to discriminate (Ekman and Friesen, 1971) even when the happy emotion is of a low intensity (Hess, Blairy and Kleck, 1997) and when the face stimuli used have degraded resolution (Johnston, McCabe and Schall, 2003) or are presented as briefly as 25 msec before being masked (Calvo and Lundquist, 2008). Adolphs (2002) has argued that facial expression is initially categorised into two superordinate categories - happy and unhappy, and then finer discrimination into subordinate categories (e.g., discriminating between two non-happy emotions such as angry and fearful) ensues.

Finally, we also replicated previous research demonstrating that emotion identification is enhanced for faces presented in the left visual field compared to the right (e.g., Bourne, 2008; Davidson, 1992) and interestingly this left visual field advantage for emotion detection was particularly pronounced for threat-related (angry and fearful) faces, a finding which supports other research implicating a superior role for the right hemisphere in the processing of threatening faces (e.g., Morris, Ohman and Dolan, 1998; Johnson and Hugdahl, 1991). There was a trend for participants to make more misclassifications of neutral faces as emotional when the neutral faces appeared on in the right visual field compared to the left. This suggests that laterality effects in face processing may extend to misperceptions or false positives as well as identification. We are currently conducting further experiments to explore this possibility.

Previous research into laterality effects in face processing in schizophrenia have produced inconsistent findings- Phillips and David (1997) presented photographs of neutral faces and happy / sad chimeric faces on-screen and asked individuals with schizophrenia and controls to rate the pleasantness of the neutral faces and to detect the emotion (happy or sad) depicted by the schematic faces. The controls made significantly more initial saccades to the left side of the faces than to the right whereas the clinical group showed the opposite pattern, making more initial saccades to the right side of the face. In contrast, Leonards and Mohr (2009) found that high magical ideation scores predict a pronounced initial saccade bias to the left side of neutral faces during free-viewing. We found no interaction between RVHS score and hemifield of false positives- in other words participants prone to visual hallucinations were no more likely than low scorers to make false positives to neutral faces on the right compared to faces on the left. Unlike the aforementioned studies, we were concerned with a possible RVHS x hemifield of misperception interaction as opposed to a RVHS x hemiface of misperception interaction which could explain why we did not find any RVHS x laterality effect. We are currently conducting further studies aimed at determining whether any RVHS x laterality interaction on accuracy and on false positive errors may be specific to hemiface rather than hemifield laterality manipulations. Future studies will also include a handedness measure to control for the differences in cerebral lateralisation and schizotypal traits that are associated with left, right and mixed handedness (e.g., Kelly and Coursey, 1992).

In conclusion, using a novel face processing task we have shown that healthy individuals who score highly on a scale measuring susceptibility to visual hallucinations have a greater tendency to misperceive neutral faces as angry than low scoring individuals. These results add to the growing weight of evidence suggesting that schizophrenia-like experiences occur in the general population, supporting the claim that symptomatic visual hallucinations lie on a continuum with normal perceptual experience.

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3. Lateral asymmetry in saccadic eye movements during face processing: the role of individual differences in schizotypy

3.1 Abstract

Healthy individuals with high as compared to low levels of schizotypal personality traits make more first saccades to the left side of faces, suggesting increased right hemisphere (RH) dominance for face processing. Patients with schizophrenia, however, show attenuated or reversed RH dominance for face processing. It is unclear whether the increased RH dominance found in high schizotypes is specific to face processing or whether it is also observable for other stimuli matched in terms of low-level visual properties. We measured gaze to faces and symmetrical fractal patterns and found higher Magical Ideation (MI) is associated with an increased left side bias for initial saccade landing points and dwell times when free-viewing faces. These laterality biases were unaffected by facial emotion. Schizotypy scores were not related to laterality biases when viewing fractals. Our results provide further evidence that high schizotypy is associated with an increase in RH dominance for face processing.

Keywords: cerebral dominance, eye movements, emotion processing, laterality, magical ideation, psychosis, schizophrenia, continuum models

3.2 Introduction

Healthy individuals show reliable right hemisphere (left visual field) dominance for face and emotion processing (Hole & Bourne, 2010). For example, Bourne (2008) used pairs of chimeric faces (in which one half of a vertically split face is neutral and the other emotional), and found that, when asked which of the two faces is the more emotive, participants showed a bias towards choosing the face that depicted emotion in the left visual field. Schizophrenia has long been associated with atypical hemispheric lateralisation (particularly attenuated asymmetry - see Crow, 1990, 1997 for reviews) and it has been argued that the behavioural manifestations of this may include impaired speech processing (see Frith, 2005) and auditory hallucinations (Barta, Pearlson, Powers, Richards & Tune, 1990; Frith, 2005).

In contrast to the left hemifield bias for face processing observed in healthy participants, patients with schizophrenia have been found to display a significantly reduced (David & Cutting, 1990), or reversed (see Kucharska-Pietura, David, Dropko and Klimkowski, 2002) laterality bias for face and emotion processing. David and Cutting (1990) asked patients with schizophrenia to decide whether happy-sad chimeric faces depicted a happy expression or a sad one. Unlike the control group who showed the expected left-hemifield bias, the schizophrenia group had no bias in either direction. A later eye tracking study (Phillips and David, 1997) found that when face stimuli are presented, laterality differences between healthy individuals and schizophrenia patients are observable from the very first saccade. Phillips and David (1997) presented faces to individuals with schizophrenia and to controls and compared the location of initial saccades. Controls displayed a significant left visual field bias for the initial saccade, while the schizophrenia group made significantly more initial saccades to the right side of the face stimuli, suggesting atypical (reversed) hemispheric specialization in the clinical group.

There is a large body of evidence in support of a symptomatic continuum between healthy individuals and those with psychotic disorders (see Verdoux & van Os, 2002). Psychotic traits are seen to varying lesser degrees in healthy individuals such as unaffected first degree relatives of schizophrenia patients, as well as high / low schizotypes (see Claridge, 1997; Eckblad & Chapman, 1983). The information processing deficits associated with schizophrenia are also present, albeit less severely, in “high schizotypes” (e.g., Park, Holzman & Lenzenweger, 1995) and there is evidence from neuroimaging studies that schizotypy and schizophrenia are associated on neurocognitive and neurophysiological levels (Aichert, Williams, Möller, Kumari & Ettinger, 2012). Importantly, the left-hemifield bias when viewing chimeric faces has been shown to be attenuated in both individuals with schizophrenia and in healthy participants with high as compared to low negative schizotypy (social anhedonia) scores (Luh & Gooding, 1999). However, the literature documenting decreased right hemisphere dominance for face processing in people with schizophrenia and high schizotypes is not consistent. For example, Leonards and Mohr (2009) found that elevated relative to low positive schizotypy (Magical Ideation) was in fact associated with an increased bias in initial saccade landing positions towards the left side of the face, suggesting that right hemisphere dominance for face processing is more prominent in high as compared to low schizotypes- this finding is in direct contrast to the clinical group in the Phillips and David (1997) study.

A number of other studies suggest that psychosis-proneness is associated with stronger than average right hemisphere dominance. For example in a free-viewing task, psychosis prone individuals rated happy – neutral chimeric faces as happier when the happy hemiface appeared in the left spatial field, and this left side / right hemisphere bias was significantly greater in the high psychosis prone group than in controls (Luh & Gooding, 1999). A similar left hemifield bias has been observed in a lateralized tachistoscopic lexical decision task in which high schizotypes were more accurate than low schizotypes at identifying target words presented to the left visual field (Brugger, Gamma, Muri, Schafer & Taylor, 1993). The left side bias, therefore, likely extends beyond face processing tasks.

The Phillips and David (1997) study was limited by small sample size (8 in the clinical group) and the Leonards and Mohr (2009) study had a number of methodological issues- specifically, the face stimuli were grayscale whereas the fractals were in colour, the two stimuli types varied in both size and orientation, and the fractals were not symmetrical whereas a face, by nature, is very near symmetrical. In addition, there may be a general left-side bias in psychosis-prone individuals that is not specific to face processing per se. As a result, it is unclear whether the Leonards and Mohr (2009) results reflect a very specific association between elevated Magical Ideation and a general left-hemifield initial saccade bias for near symmetrical images, or whether the tendency is very specific to faces.

There is evidence that the right hemisphere dominance for face processing persists across different facial emotions (Bava, Ballantyne, May, & Trauner, 2005). However, it has been proposed that the direction of laterality biases during face processing depends on the emotion depicted by the face, with the left hemisphere dominant in the processing of faces expressing positive emotions and the right hemisphere dominant in the processing of faces displaying negative affect (see Hole & Bourne, 2010). It remains unclear whether schizotypy-sensitive laterality biases when viewing faces are moderated by emotion. Such an interaction might be expected since high schizotypes respond differently to controls in emotion processing tasks. For example, high positive schizotypes are hypervigilant to threat-related emotion (Coy & Hutton, 2012) and negative schizotypes are less accurate in facial emotion classification, particularly when faces depict negative affect (Williams, Henry & Green, 2007). The aim of the current experiment is to replicate the Leonards and Mohr study with improved stimuli (faces and fractals will be matched for size, colour and orientation) and to explore any potential role of facial emotion in laterality biases. In doing so we hope to contribute to resolving the apparent discrepancy surrounding face processing laterality biases in individuals with schizophrenia and high schizoptypes.

If the Leonards and Mohr results emerged from lateral asymmetries in face processing, that are observable from the very first saccade and that are sensitive to schizotypy, then a replication of the original study is expected: higher schizotypy would be associated with an increased leftward laterality bias during face processing but not when viewing fractals. Given that positive schizotypy is associated with a hypervigilance to threat-related stimuli, and that increased arousal has been shown to affect lateral dominance, we expect to observe a schizotypy x emotion interaction whereby any effect of threat on laterality biases becomes more pronounced as positive schizotypy scores increase. Alternatively, if the results of the original study emerged from systematic differences in the low-level visual properties of the faces and fractals (which interact with schizotypy), then, with improved stimuli, we would not expect to replicate the results of the original study. Instead, we would expect no interaction between schizotypy score and stimulus type (face versus fractal).

3.3 Method

Participants*.* 35 healthy participants (19 female; mean age = 22.09 years, *SD* = 3.48, age-range = 20–34) took part in the experiment. All participants were students at Sussex University, were right handed and had normal or corrected-to-normal vision. The study was approved by the University of Sussex Psychology and Life Sciences Research Ethics Committee.

Apparatus*.* Stimuli were presented on a 22-inch CRT monitor. Eye movements were recorded using an EyeLink II head-mounted eye tracker (SR Research, Ontario) which recorded gaze at 500Hz with an average accuracy of 0.5˚. Eye event detection is based on an internal heuristic saccade detector built in the EyeLink tracker program. To detect a saccade, for each data sample, the built-in event parser computes instantaneous velocity and acceleration and a saccade is detected when these values exceed 30˚ per second or 8500˚ per second squared for two or more samples. In order to be included in our analyses, initial saccades had to have amplitudes of at least 0.5°. Trials were excluded if the initial saccade was anticipatory (latency < 80 ms) or if participants were not fixating within 0.5° of the central fixation marker at saccade onset. 92% of data were retained for analysis.

Materials*.* The stimuli comprised 24 symmetrical fractals (obtained from various freely available databases) and 96 faces (48 female) displaying numerous emotions (24 happy, 24 angry, 24 fearful and 24 neutral). The face stimuli were taken from the Radboud Faces Database (Langner *et al*., 2010). Faces and fractals were oval cropped and measured 12 x 7 cm on-screen. Each image was displayed once in colour and once in greyscale, creating a total of 240 images. Stimuli were presented in random order using Experiment Builder software (SR Research, Ontario).

Schizotypy Questionnaires.

Magical Ideation (MI) scale (Eckblad & Chapman, 1983). This is a 30 item true or false questionnaire providing a measure of Magical Ideation which is a subset of positive schizotypy.

The Revised Physical Anhedonia (PA) scale (Chapman *et al*., 1976). This 61 item (true or false) questionnaire measures Physical Anhedonia, a subset of negative schizotypy.

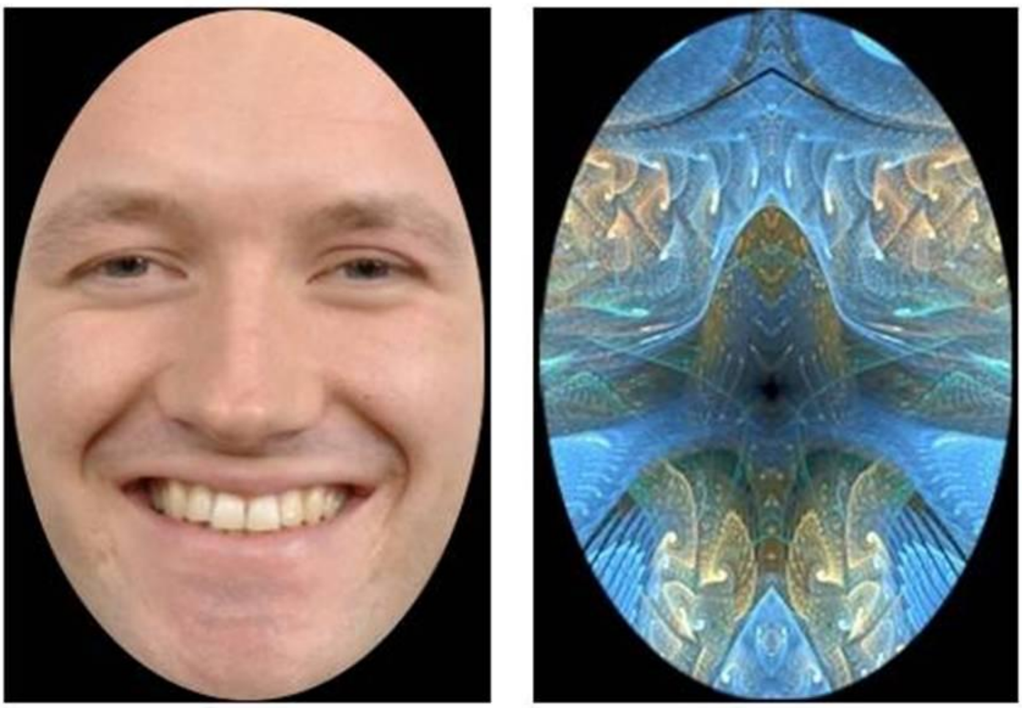

Figure 1. Example face and fractal stimuli.

Design and Procedure. All trials began with participants (seated 60 cm from the monitor) focussing on a central fixation cross. After steady fixation on the cross, a blank screen was presented for a random time period between 0 and 1250 ms (to reduce anticipatory saccades). A face or fractal image was then presented centrally onscreen for 5000ms and was then replaced with a blank screen. Participants were asked to free-view the stimuli, and to pay careful attention because there would be some questions about the stimuli at the end of the experiment. The 240 experimental trials were presented in random order across 4 blocks. The eye tracker was re-calibrated between blocks as necessary. Participants then completed the Magical Ideation (MI) scale (Eckblad & Chapman, 1983), The Revised Physical Anhedonia (PA) scale (Chapman *et al*., 1976), and the Edinburgh Handedness Inventory (Oldfield, 1971) before being fully debriefed.

Data Analysis. Eye movement data were analysed using Data Viewer Software (SR-Research, Ontario). Equal sized rectangular regions of interest (ROIs) were drawn around the left and right half of each of the stimuli. The extent of the left visual field (LVF) or right visual field (RVF) bias for initial saccades was assessed using a lateralization index (*I)* as used by Leonards and Mohr (2009):

$$I = (R - L) / (R + L)$$

Where R is the number of initial rightward saccades and the L is the number of initial leftward saccades. Positive and negative values signify a rightward and leftward bias respectively. We also calculated a laterality index for total dwell time to the left and right ROIs to provide an indication of the extent / time course of any observed laterality biases. The formula for dwell time laterality index was the same as for the initial saccade laterality index, but considered total dwell time (rather than number of initial saccades) to the left and right of the stimuli.

3.4 Results

Mean and SE laterality index scores for initial saccade and dwell time (split by stimulus type) are presented in Table 1 below.

Mean (SE) Laterality Index		
	Initial Saccade	Dwell Time
Fractal	-.138 (.05)	.019 (.03)
Neutral Face	-.103 (.60)	.046 (.04)
Happy Face	-.184 (.09)	.001 (.03)
Angry Face	-.092 (.10)	.054 (.04)
Fearful Face	-.100 (.10)	.078 (.03)

Table 1.Overall mean and standard error values for initial saccade and dwell time laterality measures split by stimulus type. N = 35.

Questionnaire scores. The overall mean MI score was 7.77 (N = 35, SD = 4.1, range = 0 - 19). The overall PA score was 11.83 (N = 35, SD = 7.2, range = 0 - 30). All participants were right handed as measured by the Edinburgh Handedness Inventory (all scores ≥ +50), but the extent of their right handedness varied (mean = 83.43, SD = 15.33, range = 50 - 100).

Despite the fact that the mean laterality index measures were similar for faces and fractals, the distribution of laterality scores varied by stimulus type and across measures (see figure 2). For initial saccade laterality index, data were centred closer to zero for fractals than for faces. The distribution was close to normal for fractals and bimodal (the majority of cases had either a clear left- or clear right-hemifield bias) for faces. In contrast, for the dwell time laterality index data, the distributions were almost equivalent for faces and fractals, and both distributions were close to normal.

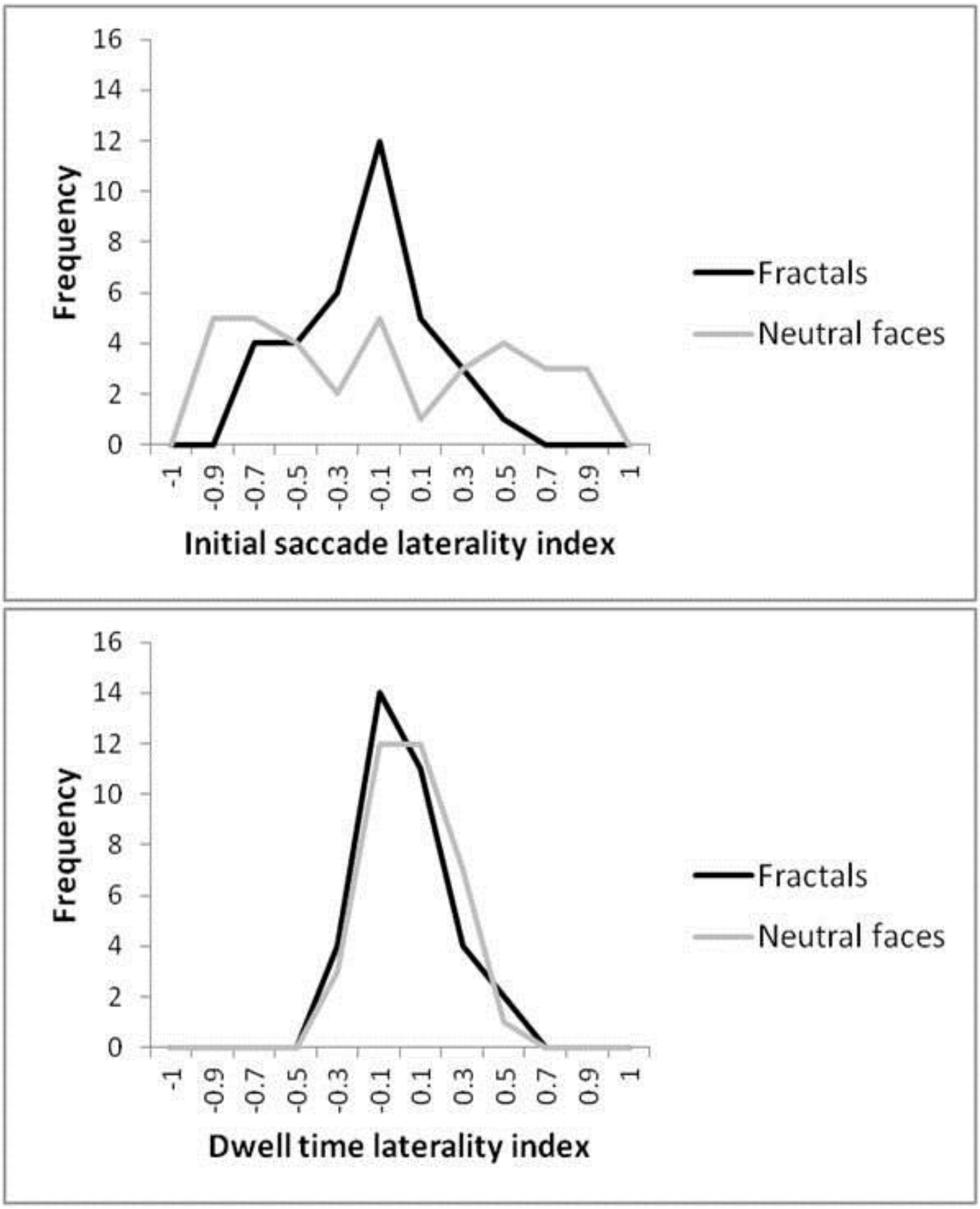

Figure 2. Frequency polygon for initial saccade (upper) and dwell time (lower) laterality index scores. The x axis consists of the mid-point values for 0.2 unit wide bins. Possible laterality index scores range from -1 (maximum leftward bias) to 1 (maximum rightward bias). N = 35.

Two one-way repeated measures ANCOVAs were performed to assess whether initial saccade or dwell time laterality measures vary systematically with stimulus type (faces or fractals). Magical ideation was entered as a covariate to assess its relationship to the two LI measures. Physical Anhedonia was also entered into the ANCOVAs initially but was not significantly related to any of the Laterality Index measures and was therefore not included in the final analyses. Handedness was also considered as a covariate to control for any confounding effects of variation in degree of right handedness. There was no significant correlation between the two covariates.

For initial saccade laterality index, there was no main effect of stimulus type $F(1,32) = .88$, ns. There was a significant interaction between the covariate magical ideation and stimulus type, $F\ (1, 32) = 5.63$, $p < .05$, $\eta^2 = .15$. Scatter plots with regression lines revealed a negative association between magical ideation and initial saccade laterality index score when viewing neutral faces, $b = -.055$, $p < .05$, $\eta^2 = .14$ (see figure 3, upper) but not when viewing fractals, $b = -.003$, ns. There was no main effect of either covariate (handedness, magical ideation), both *F*s < 3.31, *p* values > .05.

Results were replicated for the dwell time laterality measure. There was no main effect of stimulus type $F\ (1, 32) = .01$, ns. There was a significant stimulus type x magical ideation interaction $F\ (1, 32) = 4.60$, $p < .05$, $\eta^2 = .13$. Scatter plots with regression lines revealed a negative association between magical ideation and dwell time laterality index score when viewing neutral faces, $b = -.019$, $p < .05$, $\eta^2 = .14$ (see figure 3, lower) but not when viewing fractals, $b < .001$, ns. There was no significant effect of either of the covariates (handedness, magical ideation), both *F*s < 1.81, both *p* values > .05.

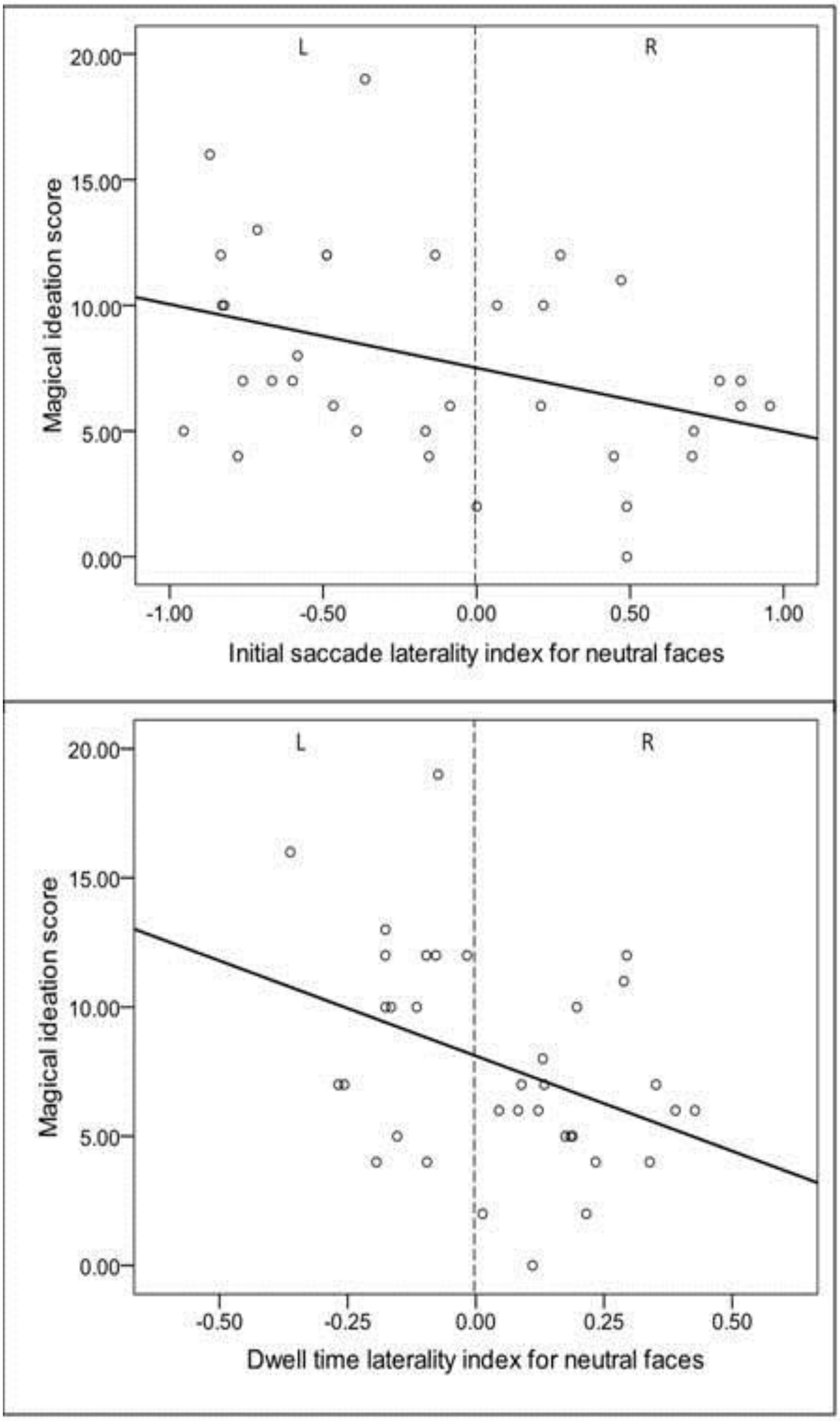

Figure 3. Initial saccade (upper) and dwell time (lower) laterality index plotted against magical ideation. Positive laterality index values represent a rightward (R) initial saccade bias. Negative laterality index values represent a leftward (L) initial saccade bias. A score of zero indicates no laterality bias and is marked with a dotted

vertical line. The best fit line has a negative slope- as MI scores increase, laterality index scores are more biased towards the left side of the neutral face stimuli.

Two further one-way repeated measures ANCOVAs (with magical ideation and handedness as covariates) assessed whether facial emotion (4 levels: neutral, happy, angry, fearful) systematically affected either laterality measure (initial saccade or dwell time). There was no main effect of emotion on initial saccade or dwell time laterality scores or any significant interactions with emotion (all *F*s < 1.26, *p* values $> .05$).

3.5 Discussion

A number of clinical studies report reduced or reversed lateralised face processing in individuals with schizophrenia (Kucharska-Pietura, David, Dropko & Klimkowski, 2002; David & Cutting, 1990), and in a very similar task to ours, Phillips and David (1997) observed greater rightward saccade / left hemisphere biases in schizophrenia patients as compared to controls when free-viewing face stimuli. Continuum models of psychosis would predict similar laterality biases in high schizotypes when viewing faces. Contrary to this expectation however, a number of non-clinical studies have shown that high schizotypy is in fact associated with an increased left side / right hemisphere bias (Leonards & Mohr, 2009; Brugger *et al*., 1993; Christie & Raine, 1988) which is in accordance with face processing laterality biases in the general population (see Levy, Heller, Banich & Burton, 1983; Leonards & Scott-Samuel, 2005). Consistent with these non-clinical studies, we found that individuals who scored highly on the Magical Ideation scale were more likely to look initially to the left half of a face and also to have increased dwell time to the left half of a face. In line with Leonards and Mohr (2009), laterality biases during face processing were not associated with Physical Anhedonia scores suggesting that it is elevated positive schizotypy in particular that is associated with increased right hemisphere involvement in face processing. Our results cannot be well explained by a general attentional bias to the left side of space because there was no difference between high and low schizotypes in laterality measures when viewing the fractal stimuli. This may suggest that positive schizotypy selectively impacts functions that are typically lateralised, such as face or language (e.g., Brugger *et al*., 1993) processing.

As pointed out by Leonards and Mohr (2009), the discrepancy between sub-clinical research and the clinical data obtained by Phillips and David (1997) may reflect qualitative differences in “symptoms” between clinical and healthy samples. The patients in the Phillips and David study were diagnosed with paranoid schizophrenia and had prevalent negative symptoms whereas in both the Leonards and Mohr study and in the current experiment schizotypy was measured from magical ideation scores. It would be interesting to assess whether healthy individuals prone to paranoid thoughts (rather than to magical thinking) have laterality biases directionally similar to the patients in the Phillips and David study. Another possible explanation for the discrepancy is confounding effects of medication on laterality biases in the Phillips and Davids study.

The fractal stimuli used in the current study were considerably more “face-like” than the fractals used by Leonards and Mohr (2009). Nevertheless, laterality biases were not observed during fractal viewing. Although faces are by nature almost symmetrical, it would be interesting to explore whether using truly symmetrical faces (e.g. right/right or left/left chimeric faces) as stimuli would derive different results. We have discussed the possibility that the association between laterality biases and schizophrenia may be dependent on the use of tasks that are lateralised (e.g., face processing / language processing), but if (for face processing at least) it is in fact specific stimulus properties such as the inherent asymmetry in the faces themselves, that is driving or triggering the observed laterality effects, then we might expect very different results with the use of perfectly symmetrical face stimuli.

Previous research has shown that psychosis proneness is associated with heightened sensitivity to threat-related material (e.g., Coy & Hutton, 2012;

Green, Williams & Davidson, 2001), but we did not observe any association between schizotypy and facial emotion for either laterality index measure. One possible explanation for the lack of an emotion effect is that the task did not require overt emotion recognition and as such the emotion depicted by the faces could be ignored without a detrimental effect on performance. Our results do suggest that any effect of facial emotion on laterality biases during free-viewing are not automatic. Future research could investigate whether emotion effects would emerge with a slightly revised task that required participants to attend to and distinguish between the different facial emotions. It would also be particularly interesting to replicate and extend the current study using combined eye tracking and functional imaging techniques in an attempt to uncover the neural correlates of our observation.

In conclusion, we provide further support for the somewhat unexpected finding by Leonards and Mohr (2009) that high positive schizotypy is associated with increased right hemisphere dominance for face processing.

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4. The influence of hallucination proneness and social threat on time perception

4.1 Abstract

Introduction: Individuals with schizophrenia frequently report disturbances in time perception, but the precise nature of such deficits and their relation to specific symptoms of the disorder is unclear. We sought to determine the relationship between hallucination proneness and time perception in healthy individuals, and whether this relationship is moderated by hypervigilance to threat-related stimuli.

Method: 206 participants completed the Revised Launay-Slade Hallucination Scale (LSHS-R) and a time reproduction task in which, on each trial, participants viewed a face (happy, angry, neutral or fearful) for between 1 and 5 seconds and then reproduced the time period with a spacebar press**.**

Results: High LSHS-R scores were associated with longer time estimates, but only during exposure to angry faces. A factor analysis of LSHS-R scores identified a factor comprising items related to reality monitoring, and this factor was most associated with the longer time estimates.

Conclusion: During exposure to potential threat in the environment, duration estimates increase with hallucination proneness. The experience of feeling exposed to threat for longer may serve to maintain a state of hypervigilance which has been shown previously to be associated with positive symptoms of schizophrenia.

Keywords: hypervigilance, internal clock, psychosis, reality monitoring, schizophrenia, schizotypy

4.2 Introduction

Individuals with schizophrenia frequently display an altered perception of time (see Bonnot *et al*., 2011; Allman & Meck, 2012 for reviews), and it has been suggested that deficient temporal information processing is related to, and may even underlie, some of the most intrusive symptoms and cognitive disturbances associated with the disorder (Posada, Franck, Augier, Georgieff & Jeannerod, 2007; Volz *et al*, 2001; Andreassen *et al*., 1999; D'Argembeau, Raffard & Van der Linden, 2008). Shergill (2005) points out that dysfunctional predictive mechanisms (a likely manifestation of deficient time processing) could lead to difficulties anticipating the consequence of one's own or of another's actions, particularly given that disturbances to the timing of perceptual, motor and cognitive processes are a likely consequence of temporally disordered information processing (Carroll, O'Donnell, Shekhar & Hetrick, 2009; Bressler, 2003). Delusions of alien control, megalomania, and verbal auditory hallucinations in schizophrenia patients may therefore be the phenomenological expression of dysfunctional neural timing (Gallagher, 2000; Haggard, Martin, Taylor-Clarke, Jeannerod & Franck, 2003; Shergill, 2005; Carroll *et al*., 2009).

Whilst a large body of evidence suggests temporal processing is disturbed in schizophrenia, the precise nature of this disturbance and its relationship to other cognitive impairments that are known to be associated with the disorder, remain unclear. Early studies (e.g., Goldstone, Boardman & Lhamon, 1959; Pearl & Berg, 1963; Wahl & Sieg, 1980) tended to find that patients with schizophrenia generally overestimate temporal durations. However, more recent research has tended to report a relative underestimation of temporal durations in schizophrenia patients (e.g., Lee *et al*., 2009; Tysk, 1983; 1990) and in those with a liability for schizophrenia (Lee, Dixon, Spence & Woodruff, 2006) as compared to controls. Carroll *et al*. (2009), however, report a significantly greater variability in the temporal estimations given by the patients as compared to the controls but no absolute difference between the two groups.

As other authors have argued, these inconsistent results are perhaps unsurprising given the generally small sample sizes and the very different methodologies used to assess temporal processing across these experiments (e.g. Davalos, Rojas & Tregellas, 2011; Bonnot *et al*., 2011). For example, some temporal tasks require visual processing during the timing intervals whereas others require auditory signals to be processed; tasks may require either prospective or retrospective time estimates, or estimates may be based on comparison, reproduction or verbal estimation. Finally the durations being estimated can vary from less than 1 second to minutes. Numerous other potential confounds and sources of variability exist in clinical populations that make it difficult to draw conclusions about the precise nature of the temporal processing deficits in patients with schizophrenia. These include, among others, differences in motivation levels and possible confounding effects of antipsychotic medication on time perception. As Walker and Diforio (1997) point out, many measures of arousal or "hypervigilance" in schizophrenia patients such as heart rate and skin conductance (which are known to impact on time perception, see Zakay, Nitzan & Glicksohn, 1983), are also likely to be affected by the patients' prescribed antipsychotic medications. Finally, patients with schizophrenia have well documented general cognitive impairments and specific impairments in working memory and attention (see Elvevåg & Goldberg, 2000 for a review) – both of which have been linked to time perception (see Elvevåg, Brown, McCormack, Vousden & Goldberg, 2004).

One strategy for avoiding such confounds that has been increasingly employed by researchers interested in studying the relationship between cognitive processes and specific psychiatric symptoms, is to use sub-clinical populations. Schizophrenia is generally assumed to be a dimensional psychopathological disorder- its signs and symptoms lie on a continuum with normal behaviour, and are seen to varying lesser degrees in healthy individuals such as unaffected first degree relatives of schizophrenia patients, as well as high / low schizotypes (see Eckblad & Chapman, 1983; Claridge, 1997). For example, healthy individuals who report hallucination-like experiences are at higher risk for developing a schizophrenia spectrum disorder (see Kelleher &

Cannon, 2011 for a review), providing support for the suggestion that a continuum exists between pathological hallucinatory symptoms and normal perceptual experiences (see also Johns & van Os, 2001). A large body of evidence has shown that the information processing deficits associated with schizophrenia are also present, albeit less severely, in high schizotypes (e.g. Park, Holzman & Lenzenweger, 1995; Barrantes-Vidal *et al*, 2003).

Despite the advantages of recruiting from healthy populations, very few studies have considered time processing using non-clinical samples. Lee *et al.* (2006) used a time bisection task in which 101 healthy participants were asked to categorise auditory tones of varying lengths as closer to short or long anchor duration. The anchor durations were either 400/800ms or 1000/2000ms. The participants were divided into high and low scorers on the Schizotypal Personality Questionnaire (SQP; Raine, 1991). Bisection points (the tone duration giving rise to 50% "long" responses) were obtained for each participant. High SPQ scorers significantly underestimated the duration of the auditory tones compared to low scorers in the 1000/2000ms bisection condition. This finding is consistent with data from schizophrenic patients using a similar bisection task (Elvevag, *et al*., 2003).

Difference in time perception between patients with schizophrenia / high schizotypes and controls can be interpreted within the framework of "Internal Clock" models of time perception. According to these models (e.g., Meck & Church, 1983; Gibbon, Church & Meck, 1984; Zakay & Block, 1996; Wearden, 2004) humans possess an internal clock which consists of a pacemaker, a switch (or gate) and a time pulse accumulator. Subjective time is based on the quantity of pulses that have been accumulated during the period being timed. The rate at which time pulses are emitted depends on a number of factors including, for example, arousal which has been shown to increase clock speed (Zakay *et al*., 1983; Wearden & Penton-Voak, 1995), resulting in time overestimations. In support of this contention, time estimates tend to be exaggerated when individuals are exposed to threat-related (more arousing) emotions such as anger and fear (Droit-Volet, Brunot & Niedenthal, 2004; Droit-Volet & Gil., 2009; Droit-Volet & Meck, 2007). Threat-related attentional biases have been shown in highly anxious individuals (see Cisler & Koster, 2010 for a review) who also tend to overestimate durations when exposed to threat-related faces during the timing interval (Bar-Haim, Kerem, Lamy & Zakay, 2010).

A large body of research suggests that high schizotypes (e.g., Fisher *et al*., 2004) and people who are prone to visual hallucinations (e.g., Coy & Hutton, 2012) are hypersensitive to threat-related emotional stimuli in the environment. It has been proposed that both hypervigilance and an altered time perception in schizophrenia may be related to or even underlie pathological experiences associated with psychosis such as delusions and hallucinations (Franck, Posada, Pichon & Haggard, 2005), but no study to our knowledge has specifically set out to assess whether hallucinatory experiences in particular (as opposed to experiences related to positive symptomatology viewed collectively) and altered time perception are associated. A number of studies have shown that versions of the Launay-Slade Hallucination Scale consist of distinct factors including some or all of the following: tendency towards visual hallucinatory experiences, tendency towards auditory hallucinatory experiences, vivid daydreams, realness of thought (reality monitoring difficulties), and hallucinations with a religious theme (see Aleman, Nieuwenstein, Böcker & De Haan, 2001; Larøi, Marczewski & Van der Linden, 2004; Morrison, Wells & Nothard, 2000; Morrison, Wells & Nothard, 2002; Levitan, Ward, Catts & Hemsley, 1996; Waters, Badcock & Maybery, 2003). Whether any association between hallucination proneness and time estimation is driven by a distinct sub-dimension of hallucination proneness would also be particularly interesting to explore. Finally, it has not been established whether there is any interaction between hallucination proneness (or particular sub-dimensions of hallucination proneness) and time processing during exposure to threatening (as compared to neutral) stimuli. The present study addresses these issues in a large sample of healthy participants, all of whom completed the Revised Launay-Slade Hallucination Scale (LSHS-R) (Morrison *et al*., 2000) and a temporal processing task in which they attempt to reproduce the length of time they were exposed to happy, angry, fearful or neutral faces. It is predicted that high hallucination prone individuals will experience a slowing of time, particularly when exposed to angry faces.

4.3 Method

Participants. 206 healthy participants (mean age = 20.2 years, *SD* = 4.03, age-range = 18.0 – 48.4; 176 female) took part in the experiment. All participants were students at Sussex University. All participants had normal or corrected-to-normal vision. The study was approved by the University of Sussex Psychology and Life Sciences Research Ethics Committee.

Materials. Stimuli consisted of 16 colour images of faces selected from the NimStim Face Stimulus Set (Tottenham *et al*., 2009). The photographs, oval cropped so that no hair or other non-facial information was visible, measured 300 x 450 pixels. For each emotion (happy, angry, fearful and neutral), 2 male and 2 female faces were used. Stimuli were presented using Experiment Builder software (SR Research, Ontario) on IBM compatible PCs with 17-inch TFT monitors.

Design. The study had a within-subjects correlational design.

Procedure. Participants were seated approximately 60 cm from the monitor. All trials began with participants focussing on a central fixation cross. A face image then appeared centrally onscreen and remained there for between 1 s and 5 s. The durations used were generated randomly prior to experimentation (6 durations were generated randomly for each 1 s time interval. The same set of durations was used for each emotion. There were 96 experimental trials split equally across emotions.

Participants were asked to focus on the face stimulus until it disappeared from screen and to try to remember how long it was there for. Text instructions then prompted participants to press and hold the spacebar for the same amount of time that the face was present for. The duration of the spacebar press (in ms) was recorded by the Experiment Builder software. While participants pressed the spacebar, a grey oval (identical in dimensions to the face stimuli) appeared onscreen. Trials were presented to participants in random order over two blocks with a short break after the first half of trials. Instructions explicitly asked participants not to count during the presentation of faces.

Participants completed the Revised Launay-Slade Hallucination Scale (LSHS-R) (Morrison *et al*., 2000) an adapted version of the original Launay-Slade Hallucination scale (Launay & Slade, 1981). The LSHS-R consists of 15 items that deal specifically with non-clinical predisposition to visual and auditory hallucinatory experiences. Each participant's trait anxiety score was also obtained from the State-Trait Anxiety Inventory (Spielberger, 1983).

Data Analysis.

In order to establish whether any association between hallucination proneness and time estimation is driven by a distinct sub-dimension of hallucination proneness, a factor analysis was conducted. To ensure that any identified factors were distinct, the Anderson-Rubin method was selected which prevents any correlation between factors. Loadings less than 0.3 were suppressed, and if a particular item loaded 0.3 or above on more than one factor then it was included only in the factor that it loaded highest on (if the difference between an items factor loadings was less than 0.1, the item was not counted in either factor). A series of Pearson correlations between identified factors and time estimates were carried out in order to determine the relationship between the identified factors and time perception.

4.4 Results

The overall mean LSHS-R score (*N* = 206) was 30.42 (*SD* = 7.87, range: 15 - 55) and the overall mean trait anxiety score (*N* = 206) was 27.73 (*SD* = 2.70, range: 20 - 34).

Data were trimmed to remove any time estimations that were more than 2.5 *SD*s above or below the mean for that trial type (e.g., happy, angry, fearful, neutral). Consequently, 81% of trials were maintained for analysis. Time estimation ratios (ratio = estimated time duration / actual duration) were calculated for each facial emotion. Values less than 1 indicate a subjective underestimation of time. The means were: angry (*M* = .7242, *SD* = .13); happy (*M* = .7212, *SD* = .14); fearful (*M* = .7222, *SD* = .13), and neutral (M = .7202, SD = .14).

A measure of the effect of emotion for each participant was calculated by subtracting their mean time estimation ratio when viewing neutral faces from their mean time estimation ratio when viewing faces of a particular emotion (e.g., index for angry = angry time estimation ratio – neutral time estimation ratio). Positive values indicate that time estimates when viewing the expressive faces were longer than time estimates when viewing neutral faces (baseline). Mean (*M*) deviation from baseline time ratios were as follows: angry (*M* = .004, *SD* = .06); happy (*M* = .001, *SD* = .06); fearful (*M* = .002, *SD* = .07). A one-way repeated measures Analysis of Variance (ANOVA) on the emotion index scores revealed no main effect of emotion on time estimation $F(3,615) = .316$, ns.

Multiple correlations (with Bonferroni adjustment applied) were conducted to assess whether hallucination proneness or anxiety scores were associated with time estimations when viewing angry, happy or fearful (as compared to neutral) faces. Hallucination proneness correlated significantly with time estimation when viewing angry faces, $r = .233$, $p < .05$. No other correlations were significant.

Factor Analysis

Factor loadings are presented below in table 1. Included items are marked with an asterisk.

The factor analysis (principle component with Varimax rotation) revealed five subscales. Three of these (Factors 1, 2 and 3) had 3 or more items loading on to them and sufficient overall reliability (Cronbach's alpha > .65) and so only these 3 were considered further. The three factors each consisted of 3 items and combined accounted for 43.75% of the variance. Factor 1 items refer to perceptual distortions, factor 2 items refer to visual or auditory hallucinatory experiences and factor 3 items refer to reality monitoring – the ability to differentiate between real versus imagined events.

ITEM	Factor 1	2	3	4	5
A passing thought will seem so real that it frightens me.			.681*		
My thoughts seem as real as actual events in my life.			.629*		
No matter how much I try to concentrate on my work unrelated thoughts always creep into my mind.				.698*	
I have had the experience of hearing a person's voice and then found that there was no one there.		.623*			
The sounds I hear in my daydreams are generally clear and distinct.		.482	.538		
The people in my daydreams seem so true to life that I think they are real.			.724*		
In my daydreams I can hear the sound of a tune almost as clearly as if I were actually listening to it.		.688*			
I hear a voice speaking my thoughts aloud.		.479		.466	
I have been troubled by hearing voices in my head.				.677*	
I have seen a person's face in front of me when no one was there.		.499*			
I have heard the voice of God speaking to me.					.876*
When I look at things they appear strange to me.	.828*				
I see shadows and shapes when there is nothing there.	.536	.464			
When I look at things they appear unreal to me.	.783*				
When I look at myself in the mirror I look different.	.503*				
Number of items	**3**	**3**	**3**	**2**	**1**
Cronbach's alpha (reliability measure)	**.724**	**.602**	**.657**	**.234**	**n/a**
Variance explained (%)	**27.81**	**8.30**	**7.64**	**7.30**	**6.98**

Table 1. Factor loadings of the hallucination proneness items. **Included items*.

In order to examine whether any of the three identified factors (perceptual distortions, visual or auditory hallucinatory experiences, or reality monitoring) are associated with time over-estimates in the threat condition, a series of correlations (Bonferroni corrected) were carried out. It emerged that only the reality monitoring factor correlated significantly with time estimation when viewing angry as compared to neutral faces, $r = .182$, $p < .05$. All other correlations were non-significant.

4.5 Discussion

In general, participants underestimated the duration of the face presentations (all time estimation ratios were < 1). Systematic underestimation of time using prospective timing paradigms (in which participants are informed of the time judgment task before the interval duration commences) is consistent with previous research (e.g., Zakay *et al*., 1983; Angrilli, Cherubini, Pavese & Mantredini, 1997; Zakay, 1993). The key finding to emerge was that higher hallucination proneness was associated with a relative lengthening of subjective time estimates, but only during exposure to the most arousing facial expression (angry). This result is consistent with previous research that has also found the effect of emotion on time estimation to be dependent on the complex interaction between how arousing the stimuli used are / the affective valence of the stimuli (Angrilli *et al*., 1997), and the type of temporal task used (Gil & Droit-Volet, 2011).

Our key finding is consistent with previous research that suggests that threat relevance and individual differences affect time processing. When effects of emotion on time perception are observed, these tend to be greatest for threat related emotions such as anger and fear in both adults (Droit-Volet *et al*., 2004; Droit-Volet & Gil., 2009) and in children (Gil, Niedenthal & Droit-Volet, 2007). Further, the threat-relevance of stimuli interacts with individual differences. Specifically, higher negative emotionality (Tipples, 2008) and increased trait anxiety (Bar-Haim *et al.*, 2010) both predict overestimations of time intervals, but interestingly in these studies the effects of these individual differences tend only to emerge in the high arousal condition (i.e., when exposed to threat-related faces during the timing interval). We did not observe an association between increased hallucination proneness and time overestimation in the fearful block, suggesting that any effect of threat on time processing observed in the current experiment is specific to a direct threat from another (angry) individual rather than some less specific type of impending threat in the environment (as indicated by a fearful face).

According to dominant models of time processing, sensitivity to arousing (e.g., threatening) stimuli has a marked effect on time estimation. These models propose that humans possess an internal clock which consists of a pacemaker, a switch or gate (see Lejeune, 1998 for discussion), and a time pulse accumulator. As an event to be timed commences, the switch or gate closes and pulses emitted from the pacemaker begin to collect in the accumulator. At the cessation of the timed event, the switch or gate opens and no more pulses accumulate. Subjective time is based on the quantity of pulses that have been accumulated during the period being timed - duration estimates increase with the number of pulses collected. Heightened arousal is said to increase the speed of the pacemaker which results in the accumulation of more pulses over a given period (hence time would be overestimated). The current results suggest that hallucination prone individuals have internal clock mechanisms that are more responsive or sensitive to the presence of threat in the environment, thus for these participants specifically, exposure to angry faces resulted in an increase in time pulse frequency.

Factor analysis of the LSHS-R confirmed that hallucination proneness is a multidimensional construct (see e.g., Aleman *et al*., 2001; Fonseca-Pedrero *et al*., 2010; Morrison *et al*., 2000; Serper *et al*., 2005; Waters, Badcock & Maybery, 2003). Questionnaire items loaded onto three distinct factors, namely: visual or auditory hallucinatory experiences, perceptual distortions and reality monitoring. It emerged that time overestimation during threat exposure is specifically related to reality monitoring (the ability to distinguish real from imagined events) an experience that often accompanies both hallucinations and hypervigilance, and is observed in Post-Traumatic Stress Disorder (PTSD), in which memories of traumatic events are experienced so vividly that the flashback experience can seem distressingly “real” (see Bremner, 2002). Interestingly, in PTSD vivid intrusive mental imagery co-occurs with an altered sense of time- for example, when a flashback is experienced, intrusive vivid imagery of a past traumatic event causes the trauma to be re-lived over and over in the present. Morrison *et al*., (2000) report that intrusive images associated with hallucinations and delusions in their schizophrenia sample were mainly related to trauma, perceived threat or fear, and argue that there are numerous similarities between psychotic experiences and intrusive re-experiencing in PTSD. Of note is the resultant hypervigilance in both disorders that may be involved in the maintenance of symptoms. Given the parallels discussed between psychosis and PTSD, it would be particularly interesting to explore common themes in the vivid imagery reported by non-clinical hallucination prone participants in order to ascertain whether these tend to be threat-relevant and / or related to past traumatic experiences. A study of this kind would have implications for psychosis interventions that specifically target amelioration of intrusive, vivid imagery. In addition, it would be interesting to investigate whether desensitisation to the angry faces may influence time estimates, and specifically whether doing so attenuates the relative temporal overestimation in those who experience vivid mental imagery / reality monitoring difficulties.

Increased activity in the autonomic nervous system has been recognised as a likely “triggering element” in the onset of psychosis (Corcoran *et al*, 2003). Stress-diathesis models of numerous psychiatric conditions such as depression and schizophrenia postulate an inextricable association between heightened subjective stress and symptom exacerbation (Gispen-de Wied, 2000; Rosenthal, 1970; Walker & Diforio, 1997). More specifically, Delespaul, DeVries and van Os (2002) report that state arousal is a strong predictor of the occurrence and intensity of hallucinations in schizophrenia patients, and the current result also suggests some association between arousal (or sensitivity to arousing emotional expression- anger) and difficulties with reality monitoring. In support of this contention, in a previous study (Coy & Hutton, 2012) we have highlighted an increased hypervigilance towards threat (a higher tolerance for false positive errors in threat detection) in high hallucination prone individuals- the tendency to misattribute anger to neutral faces in healthy individuals was more likely in those with high compared to low liability for visual hallucinations.

There was no main effect of emotion on time estimates in the current study. The majority of studies in which significant main effects of facial emotion emerge use temporal bisection tasks (e.g. Droit-Volet & Meck, 2007; Gil *et al*., 2007, but see Lee *et al*., 2011). Although it appears that bisection tasks are most sensitive to emotion effects, individual differences such as anxiety tend to interact with emotion in time reproduction tasks (e.g., Bar-Haim *et al*., 2010). Given that different temporal tasks appear to vary in terms of their sensitivity to emotion effects, it would be interesting to explore whether our results are replicated using a bisection task. The current study could be improved by increasing the number of trials in each experimental cell, and by incorporating a physiological measure of arousal (e.g. heart rate or galvanic skin response) to assess fluctuation in arousal during exposure to the different faces (e.g., threatening versus neutral).

In conclusion, our results suggest that individual differences in hallucination proneness, and more specifically in reality monitoring difficulties, are associated with a subjective slowing of time when individuals are exposed to possible threat in the environment. Viewed within the framework of internal clock models of time estimation (e.g., Gibbon *et al.*, 1984; Meck & Church, 1983; Wearden, 2004; Zakay & Block, 1996) those individuals who are more hallucination prone have a lower threshold at which the threat-related stimuli increase arousal, and therefore speed the rate at which time pulses are emitted by the pacemaker. In practical terms, it appears that psychosis-prone individuals feel exposed to potential threat in the environment for subjectively longer time periods than non psychosis-prone individuals. Importantly, this experience may itself contribute to maintaining a state of hypervigilance to social threat.

4.6 References

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